

# South American Swamp and Fossorial Rats of the Scapteromyine Group (*Cricetinae*, *Muridae*) with Comments on the Glans Penis in Murid Taxonomy<sup>1,2</sup>

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<sup>1</sup> Dedicated to Doctor ERNA MOHR in honor of her 70th birthday.

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## I. THE SWAMP AND FOSSORIAL RATS OF THE SCAPTEROMYINE GROUP (*CRICETINAE*, *MURIDAE*) OF SOUTH AMERICA

### Introduction

Scapteromyines are medium-sized to extremely large long-clawed palustrine, sub-aquatic and fossorial rodents of the subfamily Cricetinae (family Muridae). Two genera (one new) and three species, including the largest and most fossorial of living cricetines, are recognized. Scapteromyines inhabit the mixed savanna-forest regions of southern Brazil, northeastern Bolivia and much of Uruguay. They also occur in the savannas and marshes bordering the lower Río Paraná-Uruguay and its estuary in Uruguay and northern Argentina, and along the Atlantic coastal swamps, lakes and lagoons of Uruguay and Rio Grande do Sul, Brazil (map. fig. 1).

The first cricetines to invade South America, in late Tertiary, found virtually unrestricted opportunities for radiating into every possible habitat type. With exception of small and non-competitive marsupials, no small mammals had filled the niches to be exploited by the rapidly spreading and prolific cricetines. These mice advanced from north to south along the Andean foothills and from west to east across the highland plains of Bolivia and southern Brazil. From uplands they filtered into emerging river valleys particularly along the levees as natural habitats became available. Each lap or spurt in dispersal was marked by explosive radiations with successive bursts on ever higher planes of specialization. Scapteromyines comprise one of these rapidly radiating clusters which diverged from an already highly evolved cricetine stock of the southern highland plains.

The non-technical term scapteromyine is employed here in the sense of a super-genus or generic group coordinate with oryzomyine, phyllotine, sigmodont, akodont, peromyscine, etc. With fuller knowledge of cricetine origin, dispersal and radiation one or another of these natural aggrupations of closely related and nominal genera may be consolidated into a single well defined genus. Others may be accorded formal tribal rank within the subfamily Cricetinae.

### Material

The present review grew out of an attempt to determine the systematic position of the first specimens of *Mus tomentosus* Lichtenstein, 1830, to arrive in a North American Museum. Two study skins and skulls sent to the Chicago Natural History Museum



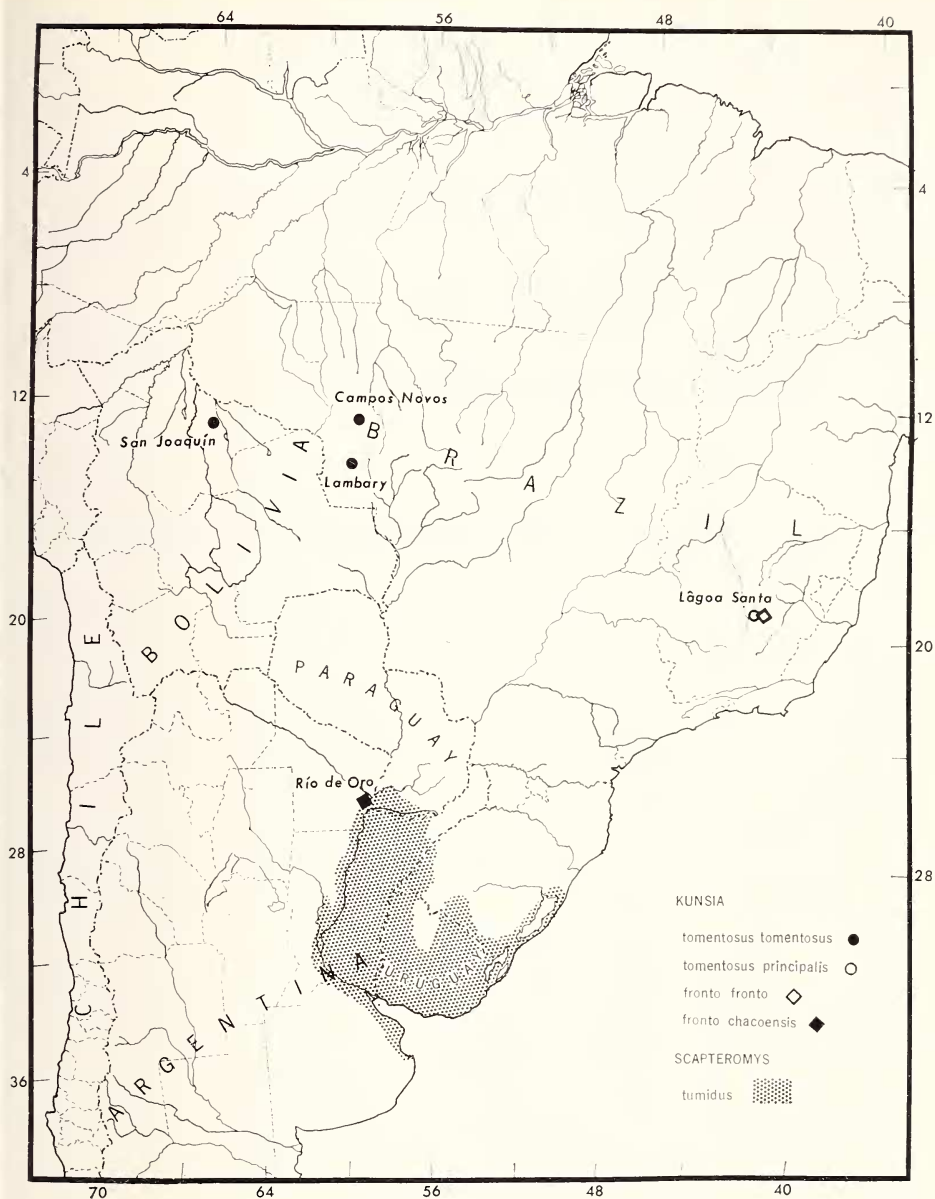


Fig. 1. Map, distribution of the species and subspecies of scapteromyine rodents.

for identification, were collected in October and December, 1963, by personnel of the Middle America Research Unit (MARU) during the course of their investigations of hemorrhagic fever in the San Joaquín region, Beni, Bolivia. At that time there was available for comparison in the Chicago Natural History Museum only a single topotype of the nearly related *Scapteromys aquaticus* Thomas (= *S. tumidus* Waterhouse).

In response to my urgent requests for additional study material, a total of 145 specimens was sent me by the scientific institutions and individuals listed below.

*Mus tomentosus* Lichtenstein

Type (skin and skull), Zoologisches Museum, Berlin, loan.

*Scapteromys gnambiquarae* Miranda Ribeiro

Cotype (skull only), British Museum (Natural History), loan.

*Scapteromys chacoensis* Gyldenstolpe

Type (skin and skull), Naturhistoriska Riksmuseet, Stockholm, loan.

*Scapteromys tumidus*

American Museum of Natural History, loan, 122 specimens (skins and skeletons, 16 in alcohol).

British Museum (Natural History), loan, 11 specimens (skins and skulls).

Museo de La Plata, Argentina, exchange, 4 specimens (skins and skulls).

U. S. National Museum, loan, 1 specimen (skin and skull).

Professor Dr. RAUL VAZ-FERREIRA, Montevideo, Uruguay, gift, 4 specimens (skins and skulls).

### Acknowledgments

This account of scapteromyine rodents could not have been undertaken without the cooperation of the authorities of the institutions listed above. For their prompt and generous assistance I am particularly grateful to Dr. GORDON B. CORBET of London, Dr. DAVID JOHNSON and Dr. CHARLES O. HANDLEY, Jr., of Washington, Professor Dr. J. A. G. JOHNELS of Stockholm, Dr. G. H. W. STEIN of Berlin, Dr. RICHARD VAN GELDER of New York and Professor Dr. RAUL VAZ-FERREIRA of Montevideo.

The specimens of *Scapteromys* made available to me for study by the American Museum of Natural History were collected during the course of field work conducted by that institution under a Grant from the U. S. Army Medical Research and Development Command (Grant DA—MD—49—193—63—G 82). My appreciation and gratitude is expressed to the Department of Defense for its sponsorship and support of research leading to a better knowledge of native faunas and host-parasite relationships.

The illustrations are the work of the Chicago Natural History Museum's staff artist MARION PAHL and Photographers JOHN BAYALIS and HOMER V. HOLDREN. The drawings for figures 1, 7, 11—13 were made by Miss JOSEPHINE STESSL.

### Abbreviations

The following abbreviations for names of institutions are used in the text and lists of specimens examined:

AMNH	=	American Museum of Natural History
BM	=	British Museum (Natural History)
BZM	=	Zoologisches Museum der Humboldt Universität, Berlin
CNHM	=	Chicago Natural History Museum
NRS	=	Naturhistoriska Riksmuseet, Stockholm
USNM	=	United States National Museum

## Scapteromyine Group

### Characters

External. — General size and form rat-like with adaptations for palustrine, semi-aquatic and fossorial life; color somber, never reddish, pelage soft or harsh but not hispid; facial vibrissae comparatively short; tail (fig. 2) shorter than combined head and body length; ears (fig. 3) well rounded, length from notch always more than one-half length of hind foot; fore and hind feet (figs. 4, 5) comparatively large and powerful, claws elongate and approximately equal to or longer than their respective digits measured on dorsal surface, vestigial pollex with sharp or nail-like claw, fifth digit (less claw) extending to base of second phalanx of fourth digit; outer digits of hind foot short, the first (less claw) not extending to base of first phalanx of second, the

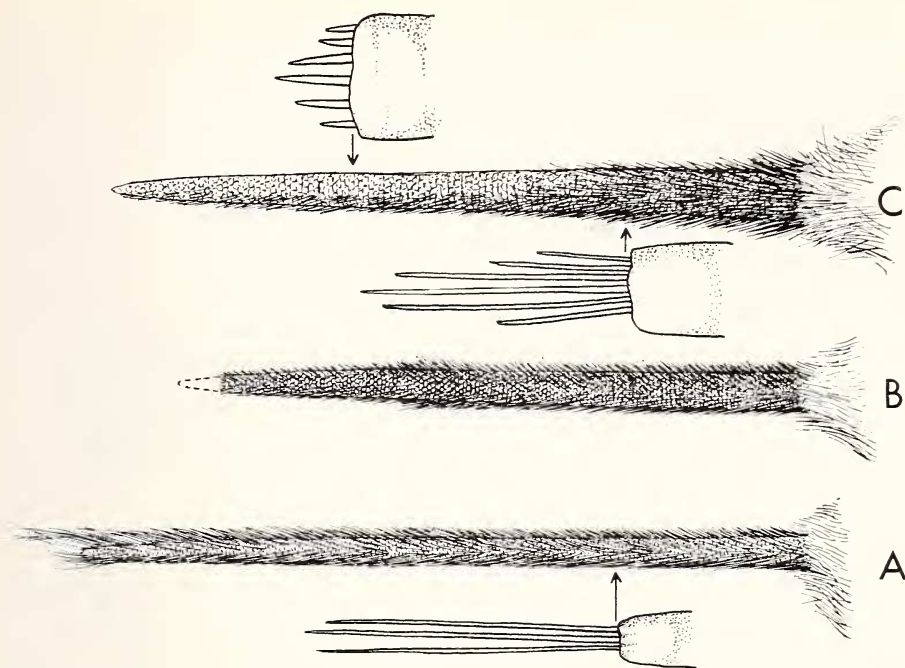


Fig. 2. Tails of scapteromyines, from dry study skins, lateral aspect: A. *Scapteromys tumidus*; B. *Kunsia fronto chacoensis*; C. *Kunsia tomentosus*. Scales and corresponding hairs from dorsal and ventral aspects as shown, greatly enlarged.

fifth barely reaching or extending slightly beyond base of first phalanx of fourth; heel hairy, plantar surface naked, largely scutellated, plantar tubercles 5 or 6, the first postdigital and metatarsal pads always well developed; mammae, 2 pectoral, 1 abdominal, 1 inguinal = 8.

Cranial (pls. 6, 8–15). — Dorsal contour of skull weakly convex with crest of supraoccipital raised slightly above plane of nasal tips; anterior process of premaxillary projected slightly or not at all beyond antero-vertical plane of incisors and never united with anterolateral border of nasals to form a tubular projection or trumpet; nasals tapering behind to a point or truncate with a short median process often present; supraorbital region narrow and constricted mesially, width at mid frontal plane less than greatest breadth of rostrum; supraorbital edges square and without beading, ridges or ledges but a rudimentary postorbital process present or absent; dorsal anterolateral processes ("horns") of parietal well developed; interparietal small but well developed, its greatest width about two thirds or less greatest distance across common parietal suture and approximately equal to width across frontoparietal suture; zygomatic arches complete, zygomatic plate high, wide and projecting well forward of antorbital bridge, its anterior border concave with dorsal corner rounded or pointed but not produced as a distinct spine; antero-posterior width of zygomatic plate more than one-half least interorbital breadth; dorsal opening of antorbital foramen ovate in outline and deeply excised exposing nearly full width of zygomatic plate when viewed from above; incisive foramina long, narrow, pointed fore and aft and produced posteriorly to or slightly beyond anterior plane of first molars; palatal bridge long and extending to or behind posterior plane of last molars, the hind border rounded or square with or without a short median

spine; posterolateral palatal fossae absent or rudimentary, posterolateral palatal pits small and rounded or slit-like; outline of mesopterygoid fossa U- or M-shaped, width at base of hamular processes equal to or greater than width of parapterygoid fossa measured at same plane; pterygoid processes more or less parallel-sided; parapterygoid fossa as seen from ventral surface, shallow roughly trapezoidal in outline, its anterior wall flattened and never undercut to form a deep pit; sphenopalatine vacuities large, lateral wings of basisphenoid and presphenoid thinly ossified and largely fenestrated; bullae moderately inflated their greatest anteroposterior axis less than alveolar length of molar row.

**Dental** (fig. 6; pls. 16–19). — Incisors moderately developed and not notably specialized, orthodont to slightly opisthodont, outer surfaces ungrooved; upper molar rows more or less parallel-sided, molars subhypsodont, unworn occlusal surface slightly terraced or plane with enamel pattern of first two upper and lower molars E- or S-shaped, i. e., tetralophodont or trilophodont, never bilophodont or 8-shaped; postcingulum reduced or obsolete and undefined in moderately worn molars; vestigial mesoloph discrete or completely fused with paracone; mesolophid absent or present in unworn  $m_{1-2}$  and fused with entoconid in worn; paralophule when present in  $m_{1-2}$  fused with mesostyle; entolophulid, if present, fused with mesostylid and/or mesolophid; enteroloph absent, ectostylid absent or poorly developed; anterolabial style, if present, fused with anteroloph.

**Phallic.** — The glans penis of *Scapteromys* is described in Section II (p. 131, figs. 10–13).

### Comparisons

The stout, long-clawed fore and hind feet distinguish scapteromyines from all cricetines except some oxymycterines<sup>3</sup> and the akodont *Notiomys*. The latter consists of considerably smaller animals with differently formed head and skull (pls. 1–4). The

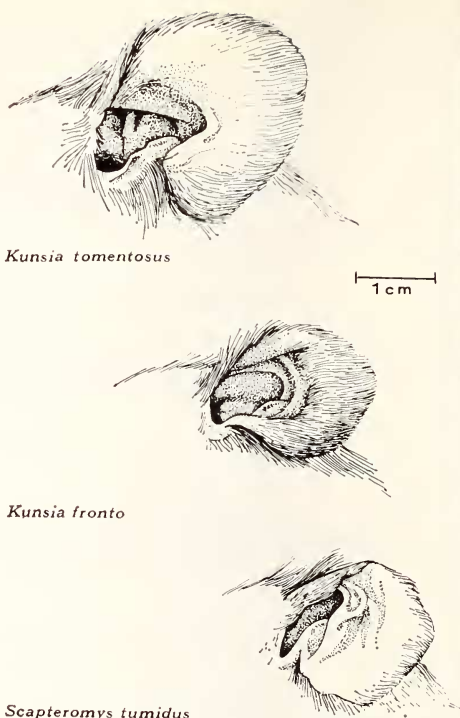


Fig. 3. Ears of scapteromyines. *Kunsia tomentosus* and *K. fronto* from dry study skins, relaxed; *Scapteromys tumidus* from spirit preserved specimen.

<sup>3</sup> Oxymycterines include *Oxymycterus* (pls. 1–4), *Podoxomys*, *Lenoxus* and *Abrothrix*. *Microxus mimus*, type species of *Microxus*, is an *Abrothrix*. "*Microxus*" *iheringi*, first described as *Oxymycterus iheringi* Thomas, is a local form of *Oxymycterus rutilans*. Oxymycterines are preeminently insect, worm and grub eaters. They are nearest related to *Akodon* (sensu lato) but the line between the two is tenuous. The group is characterized by smooth, low-domed skull; long, narrow rostrum with nasals and premaxillaries produced well beyond anterior plane of incisors and forming a tube or trumpet; zygomata weak but complete, low slung and hardly spreading beyond lateral plane of braincase; zygomatic plate degenerate with pronounced slope backward and outward, its greatest anteroposterior width less than one-half interorbital breadth; interorbital region rounded without beading or ridges, its least breadth more than greatest width of rostrum; antorbital foramen with slight dorsal excision, antorbital bridge



oxymycterine *Podoxomys* and *Abrothrix* are likewise smaller with distinct cranial characters while the fore claws of *Abrothrix* are much shorter. Large species of *Oxymycterus* and *Lenoxus apicalis* are comparable in size to *Scapteromys tumidus*. Adults of *Oxymycterus* spp., however, are more uniformly colored rufous throughout with the ochraceous underparts little defined from sides, ears smaller and tail without pencil or specialized keel hairs. *Lenoxus*, like *Abrothrix*, is comparatively short clawed, nearly uniformly drab with pelage of underparts thin, tail sparsely haired with terminal one-fifth to one-third nearly bare and unpigmented. Scapteromyines differ further from all oxymycterines and true akodonts chiefly by the strong zygomatic, stout, extremely wide and nearly erect zygomatic plate with anterior border concave, deep incision of antorbital foramina as seen from above, rostrum terminating at vertical plane of incisors without formation of trumpet, interparietal comparatively well developed (pls. 1—4), ectolophid absent or extremely small.

Scapteromyines are distinguished from sigmodonts principally by absence of spine on anterodorsal corner of zygomatic plate and relatively simple or unexcavated posteropalatal region. Cranial distinction from phyllotines depends on a combination of characters. In specific cases, any one of a number of gross cranial characters separates any species of scapteromyine from any phyllotine species (cf. HERSHKOVITZ, 1962: 116—121 et seq.). The diagnostic dental characters of scapteromyines as compared with all other living cricetines are upper incisors orthodont, molars tetralophodont, enteroloph absent, ectolophid absent or rudimentary, mesoloph reduced and fused with paracone except in unworn m<sup>3</sup>. The typical feature of the moderately worn molar of scapteromyines is the broad middle loph (II of upper, IV of lower) bifurcated at margin into a large lobe (paracone or entoconid) and a small lobe (paralophule + mesostyle or entolophulid + mesostylid), fig. 6).

The glans penis of *Scapteromys* with its bilobate, convergent and fused lateral bacular digits (fig. 10—13) is unique among murids so far as known. Phallic characters of *Kunsia* are unknown.

### Adaptive Radiation

(Plates 1—4)

Adaptive radiation among scapteromyines begins with a hypothetical palustrine and subfossorial ancestor and leads ultimately to aquatic descendants on one hand and to obligate fossorial issue on the other. *Scapteromys* pursues the first line of evolution while *Kunsia* (gen. nov.) has already gone further than all other cricetines along the second.

When the ancestral scapteromyine reached the highland plains of eastern Bolivia or the planalto of southern Brazil, it was equipped for the exigences of life in floodlands during rainy periods and for surviving drouth and famine in dry periods. Increasing aridity in the seasonally dry Brazilian-Bolivian uplands accelerated the evolution of specializations for grinding and digesting dry tough grasses and shrubs

short, narrow with strong downward deflection; dorsal and lateral frontal sinuses well inflated; interparietal reduced; incisive foramina elongate, extending posteriorly behind anterior plane of first molars; palate long, wide and relatively uncomplicated; mesoptergoid fossa broad and wider than parapterygoid fossa measured at base of hamular processes; parapterygoid fossa shallow, not undercut or excavated anteriorly; sphenopalatine fissures or vacuities small or absent; mandible weak, elongate, angle longer than high, capsule of incisor root not forming a projecting tubercle; incisors weak with outer surface pale, the upper short and orthodont to opisthodont, the lower slender and pointed; molars small, hypsodont, occlusal surface crested to terraced; enamel pattern tetralophodont in unworn to bilophodont or 8-shaped in worn; second upper molar always longer than wide.

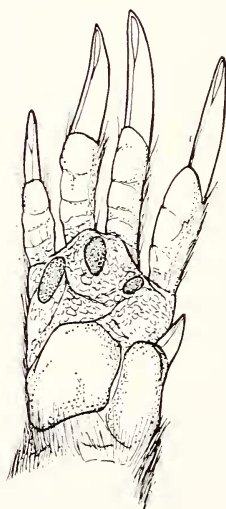
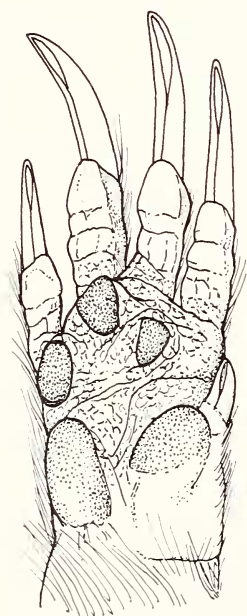
*Kunsia tomentosus**Kunsia fronto**Scapteromys tumidus*

Fig. 4. Fore feet of scapteromyines, dorsal and ventral surfaces. *Kunsia tomentosus* and *K. fronto* from dry study skins, relaxed; *Scapteromys tumidus* from spirit preserved specimen.



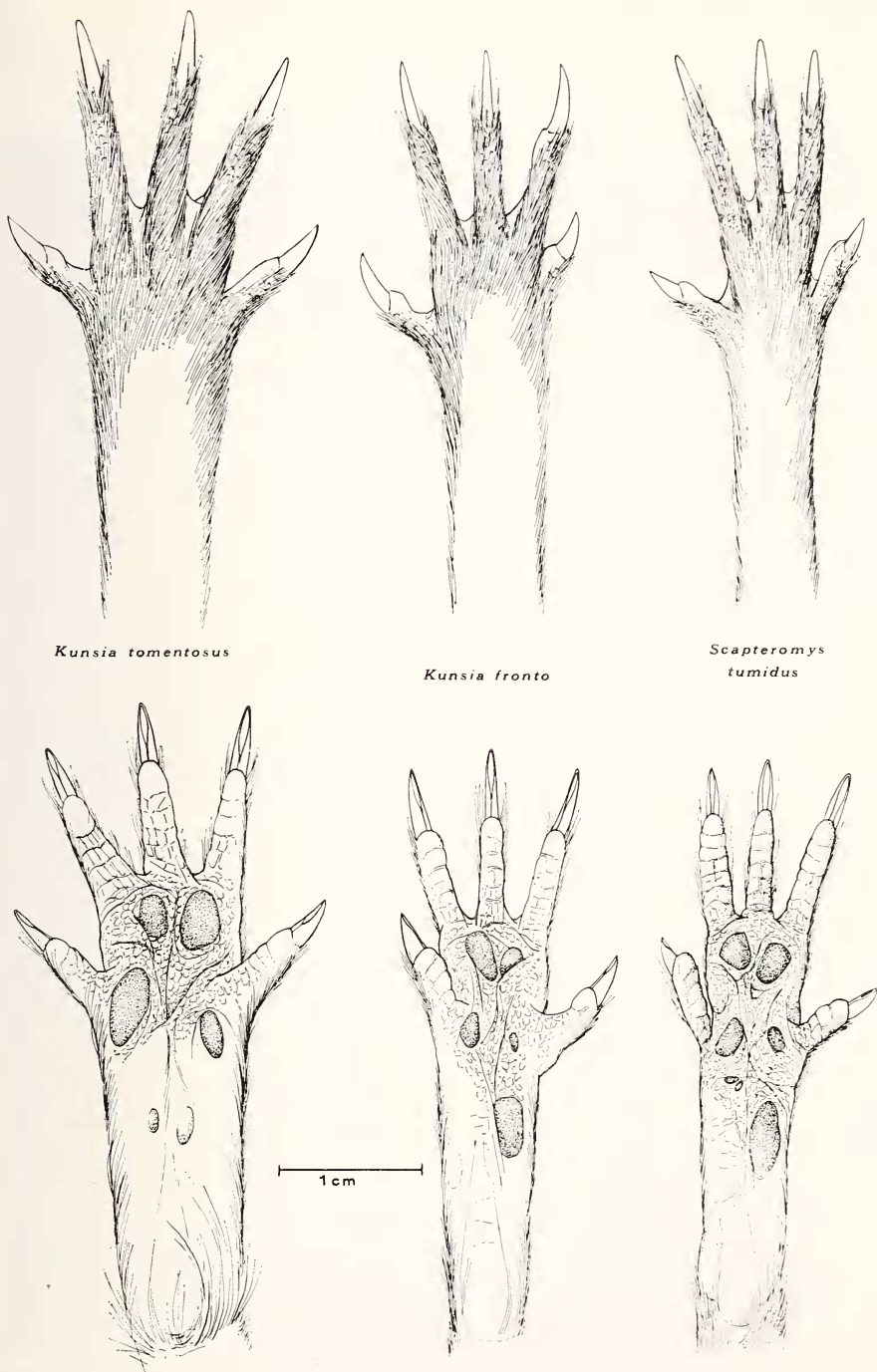


Fig. 5. Hind feet of scapteromyines, dorsal and ventral surfaces. *Kunsia tomentosus* and *K. fronto* from dry study skins, relaxed; *Scapteromys tumidus* from spirit preserved specimen.

found above ground and for burrowing beneath in search of tender roots, annelids, arthropods, and other invertebrates. Burrows and tunnels also served as refuges from predators and dessicating heat and winds. All the while, continued emergence and broadening of the flood plains through uplift and sedimentation of the Paraná River

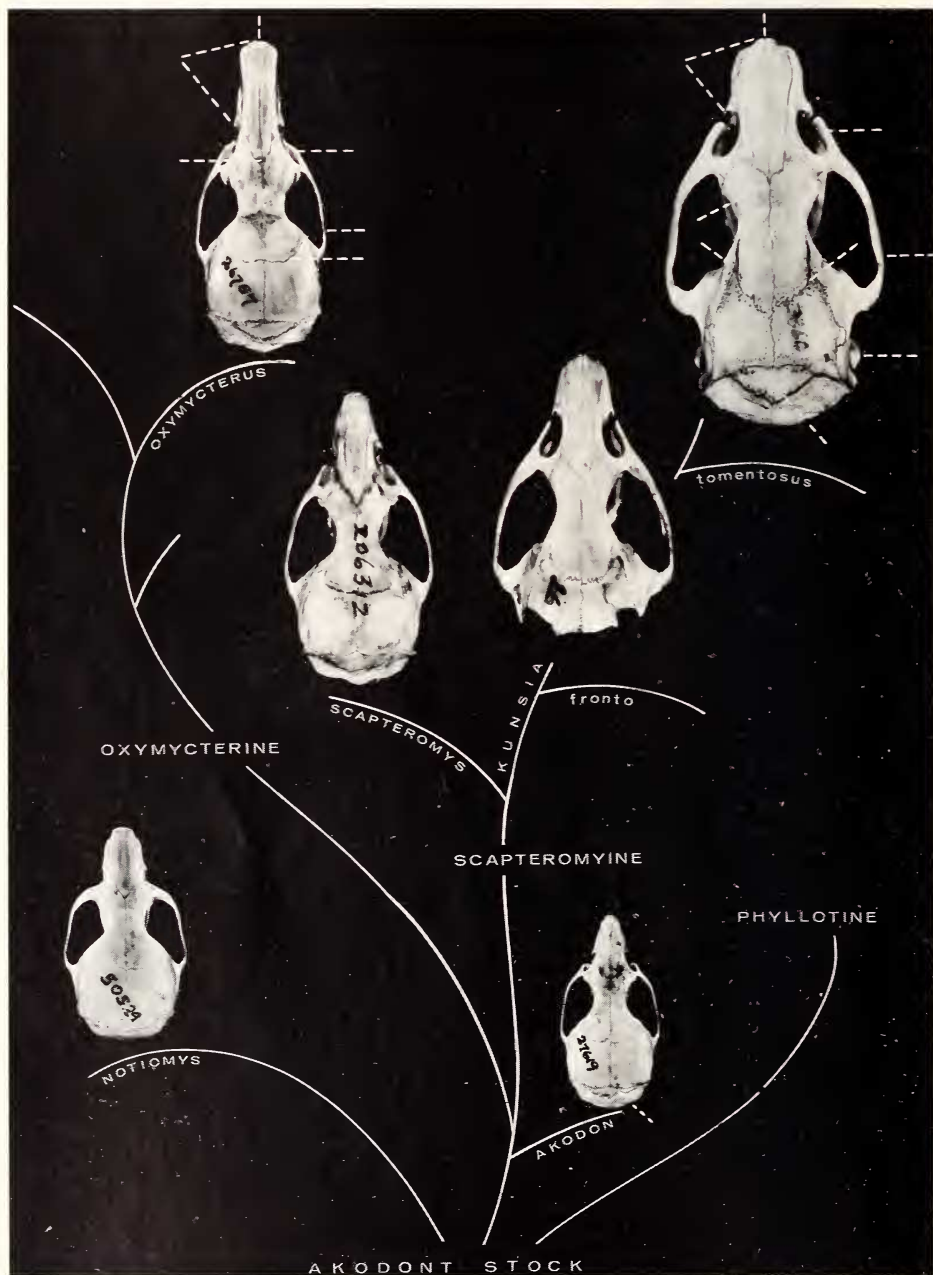


Plate 1. Phylogeny and cranial evolution of scapteromyines and the related long-clawed *Oxymycterus* and *Notiomys*: Dorsal aspect of skulls.

basin furnished new habitats for animals of the bordering highlands and gave impetus to the evolution of palustrine and aquatic forms.

The long digging claws, comparatively short tail, high and wide crowned molars and well formed zygomatics with broad, forward projecting zygomatic plate of the hypothetical scapteromyine ancestor are preserved, perhaps with little modification

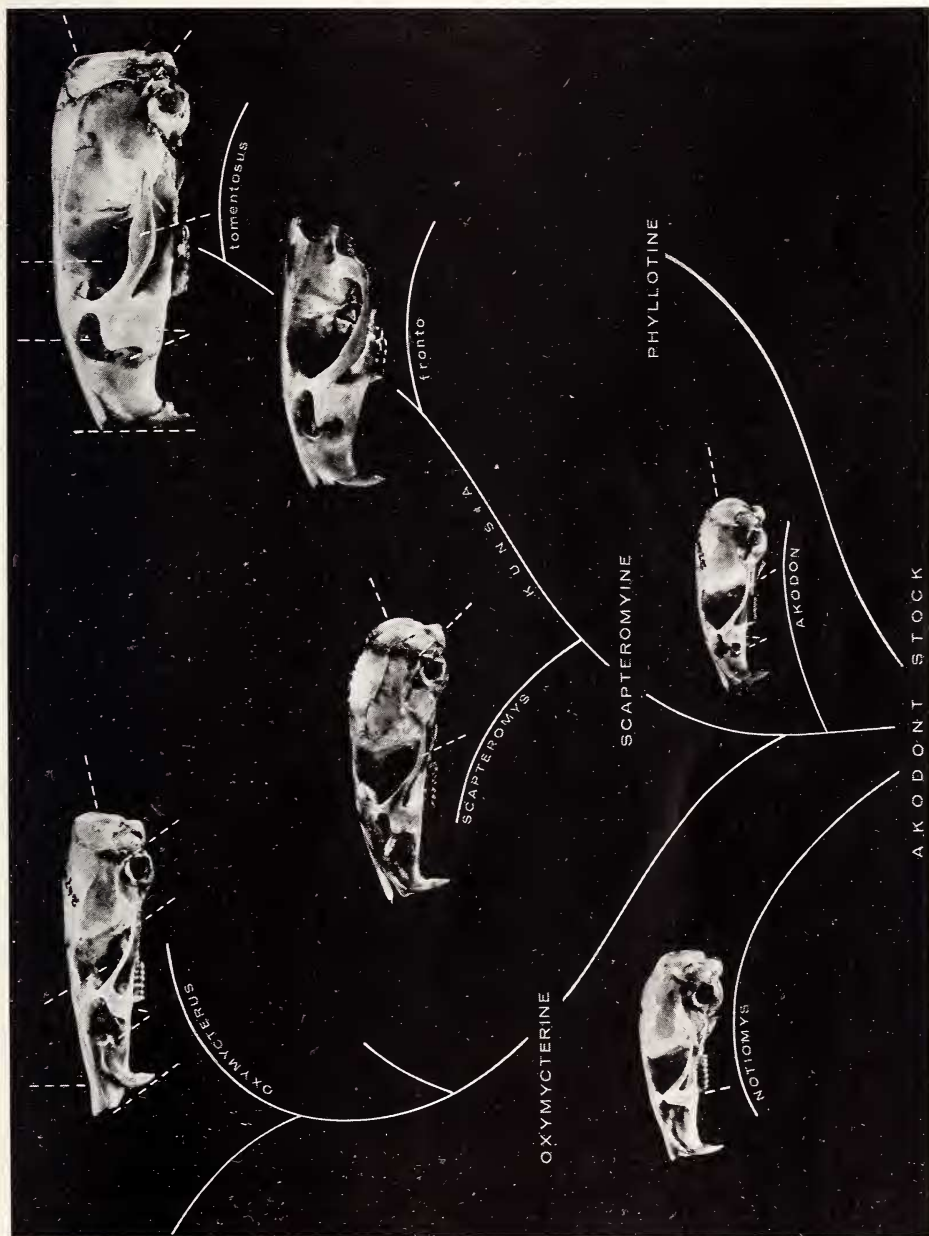


Plate 2. Phylogeny and cranial evolution of scapteromyines and the related long-clawed *Oxymycterus* and *Notiomys*: Lateral aspects of skulls.

in the single living species of *Scapteromys*. On the other hand, the thick water repellent pelage, oarlike hind feet with interdigital webbing and the caudal keel hairs of *Scapteromys* are newly evolved aquatic characters. In the frankly fossorial *Kunsia*, the comparatively simple digging ancestral equipment has become more highly specialized than in other cricetines. The pelage has become thinner and coarser, fore and hind feet thicker and stronger, claws longer and heavier, digital bristles longer and

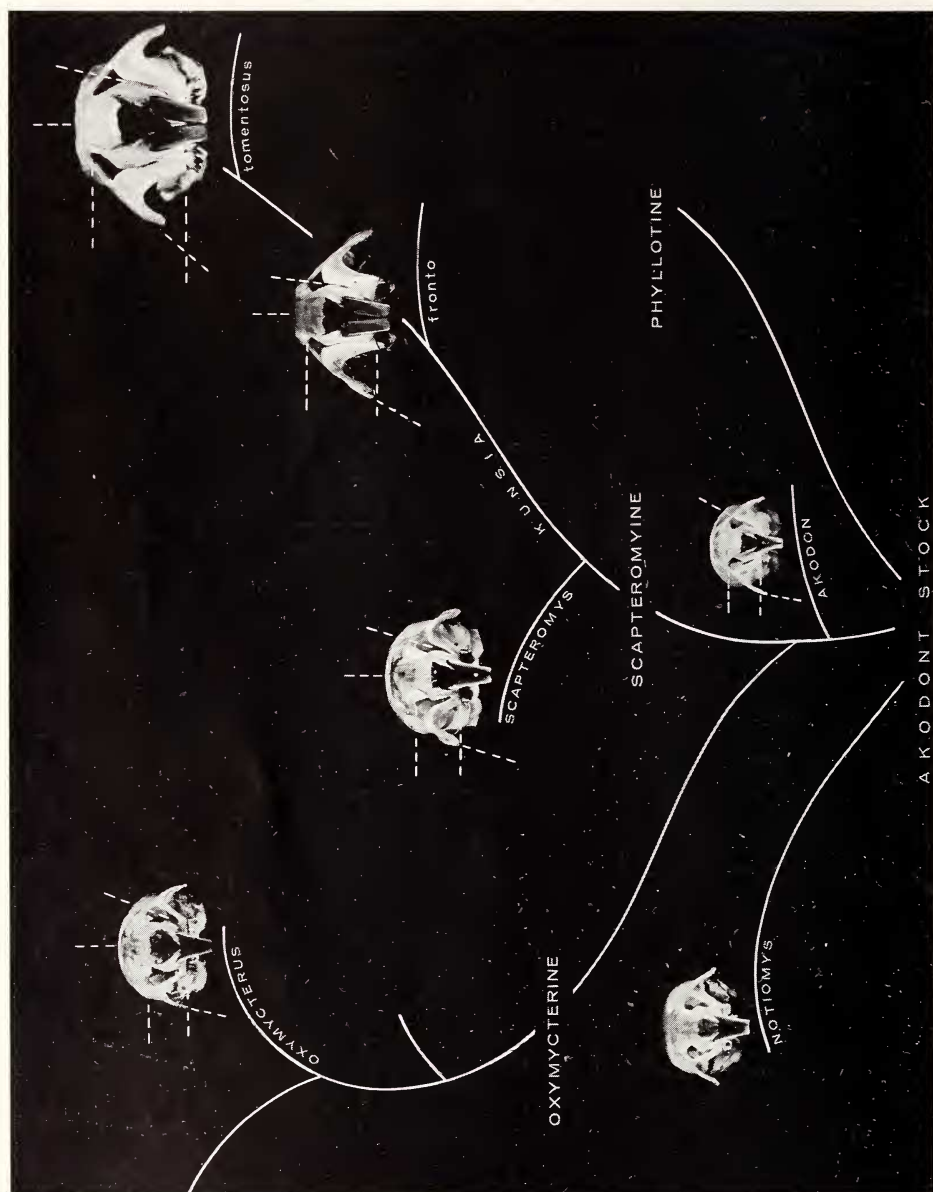


Plate 3. Phylogeny and cranial evolution of scapteromyines and the related long-clawed *Oxymycterus* and *Notiomys*: Anterior aspect of skulls. Note position and angle of zygomatic plate relative to horizontal plane of palate and top of skull.

thicker, ears smaller, tail shorter with scales coarser and pelage sparser, stiffer and shorter (fig. 2—5). Cranially, the muzzle has become heavier, with a pronounced downward inflection, the nasals shorter and broader throughout, their proximal ends less tapered and extending slightly or not at all behind fronto-maxillary sutures. In addition, parietal and occipital crests have made their appearance, the occipital bone

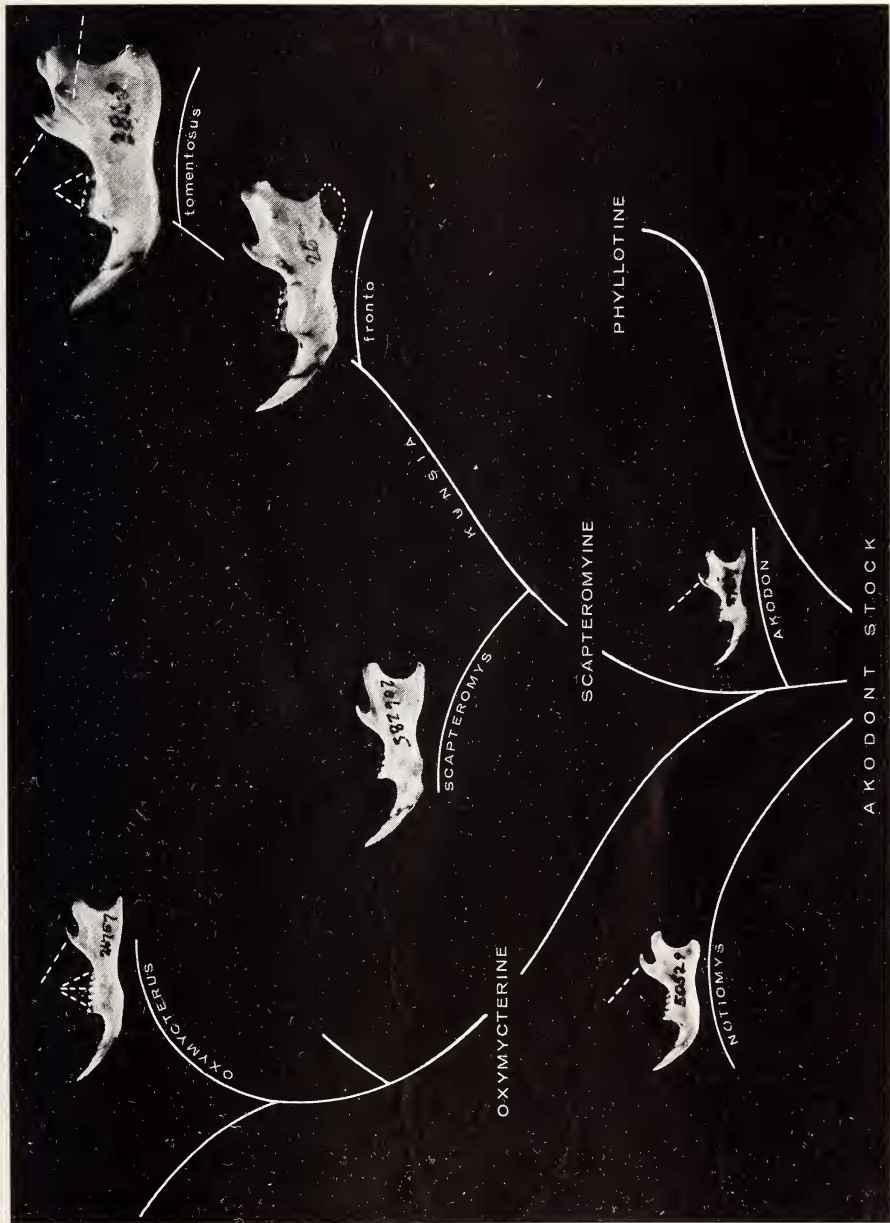


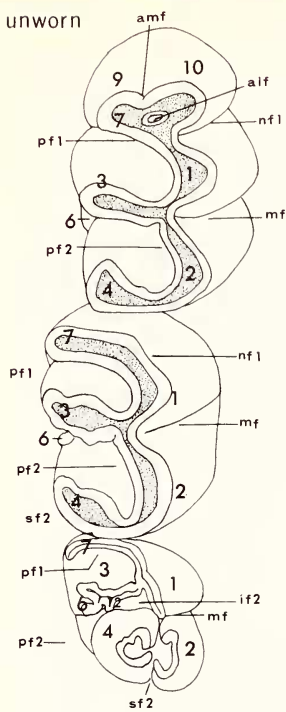
Plate 4. Phylogeny and cranial evolution of scapteromyines and the related long-clawed *Oxymycterus* and *Notiomyis*: Mandibles.



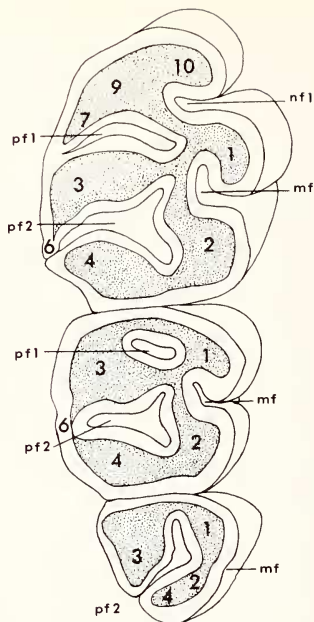
# KUNSLIA TOMENTOSUS

unworn

worn



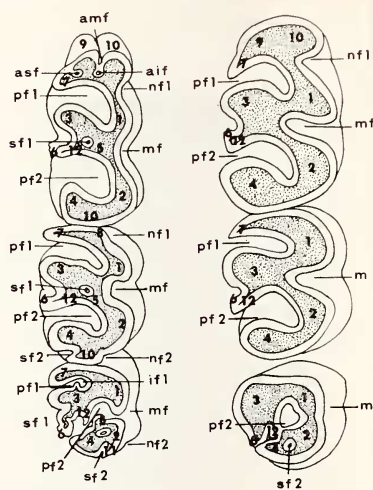
UPPER RIGHT



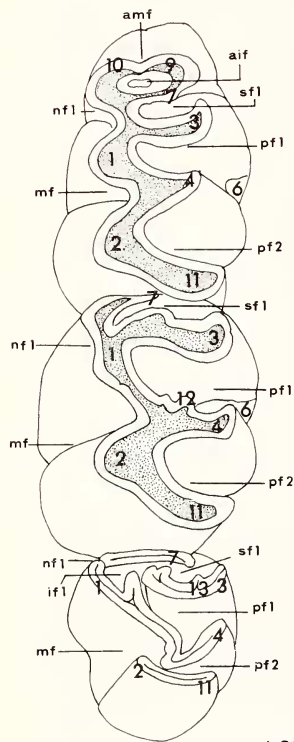
# SCAPTEROMYS TUMIDUS

unworn

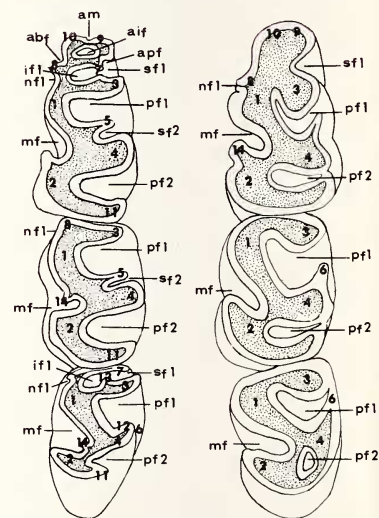
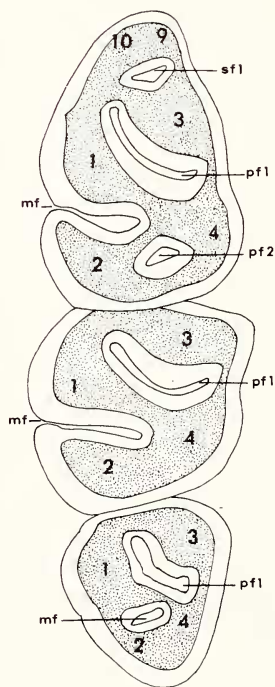
worn



UPPER RIGHT



LOWER LEFT



LOWER LEFT

Fig. 6. Molars of *Kunsia tomentosus* and *Scapteromys tumidus*; Enamel pattern of unworn and worn upper and lower crowns. For explanation of symbols see page 95.



has inclined forward, the zygomata have become heavier, more outspread and raised, the jugal broadened and strengthened. Dentally, the upper incisors have become heavier but short of true seizer-digger proportions (cf. HERSHKOVITZ, 1962:102) and the molar pattern has become more simple with obsolescence of the postcingulum, reduction and obsolescence of the mesoloph and tendency for the pattern of the occlusal surface of the lower molars to become S- rather than E-shaped.

Fossorial cricetines, like fossorial rodents in general, are of two functional types. The first is shrew- or mole-like superficially but with weak teeth and jaws and is primarily insect and worm eating. The second is pocket gopher-like with strong teeth and jaws and is primarily grass, forb and root eating. *Kunsia* is the outstanding, if not the only living gopher-like cricetine. Soricine or talpine cricetines are represented by neotropical oxymycterines and many akodonts, most notably the monotypic *Blarinomys*. They are characterized by thick, soft pelage, weak zygomata and mandible. They are generally small and wiry. Gopher-like rodents are comparatively large and stocky and nearly all their specialized characters, detailed in the above description of *Kunsia*, contrast with those of the soricine type.

*Scapteromys*, the other arm of the primary dichotomy in scapteromyine evolution is progressively becoming more adapted for aquatic life. Its present grade of evolution, however, equips *Scapteromys* less for a specialized aquatic way of life than for survival at times when no other way of life is possible. So far as known, *Scapteromys* does not prefer fish, molluscs or other highly specialized aquatic fare. Its comparatively weak incisors are better designed for cutting worms and grubs while the less simplified molars with persistent or vestigial mesolophs (id) can break only the weaker shells of arthropods. Its fossorial characters such as the long strong claws persist but may be diverted to other uses. Tree climbing, facilitated by these sharp and recurved digging claws, may still be as valuable to *Scapteromys* for survival as is swimming.

Aquatic adaptations in the ancestral scapteromyine may never have been advanced and they play no important role in the economy of *Kunsia*. Evolution of *Kunsia*, therefore, is more nearly in line with that of the dominantly fossorial ancestral form. On the other hand, *Scapteromys*, more primitive than *Kunsia* in most respects, has diverged more widely in leaving the digging habitus for the swimming and climbing.

#### Explanation of Figure 64. Names of Enameled Elements

##### Upper Molars

1. Protocone
2. Hypocone
3. Paracone
4. Metacone
5. Mesoloph
6. Mesostyle
7. Anteroloph
8. (Anteroconule)
9. Anterolabial conule
10. Anterolingual conule
11. Posteroloph
12. Paralophule
13. (Enteroloph)

##### Lower Molars

1. Protoconid
2. Hypoconid
3. Metaconid
4. Entoconid
5. Mesolophid
6. Mesostylid
7. Anterolophid
8. Anteroconulid
9. Anterolingual conulid
10. Anterolabial conulid
11. Posterolophid
12. Enterolophulid
13. Metalophulid
14. Ectolophid

#### Names of Folds

- pf 1 First primary fold
- pf 2 Second primary fold
- sf 1 First secondary fold
- sf 2 Second secondary fold
- mf Major fold
- nf 1 First minor fold
- nf 2 Second minor fold

- if 1 First internal fold
- if 2 Second internal fold
- amf Anterior median fold
- asf Anterior secondary fold
- alf Anterior labial fold
- apf Anterior primary fold
- aif Anterior internal fold

<sup>4</sup> See HERSHKOVITZ (1962: 69—115) for an account of cricetine molar evolution and a detailed description of the enamel pattern.

### Relationships

Scapteromyines appear to be nearest related to phyllotines and oxymycterines and together they probably arose from a common akodont stock. In radiating into the aquatic niche *Scapteromys* followed a path which partly parallels that of the phyllotine genus *Pseudoryzomys* and the oxymycterine *Oxymycterus*. Resemblance to the latter extends also to burrowing habits and diet. Fossorial *Kunsia* has no ecological equivalent among phyllotines or oxymycterines but is most nearly approached in this respect by the similarly long-clawed but more distantly related *Notiomys*.

### Incertae sedis

Of the three species discussed below, the first, *Mus fossorius* Lund may be a scapteromyine but the remaining two, originally described as species of *Scapteromys*, do not belong here. Determination of their true generic position requires examination of the types.

*Mus fossorius* Lund (1841: 276, 280, 281) from Lagôa Santa, Minas Gerais, Brazil, is described as follows, freely translated from the Danish:

(Page 276) "Among the genera of rodents I must consider two living forms known from skeletal parts found in the caves. One I denominate *Mus principalis* because it is larger than all others. The second I call *Mus fossorius* because the extraordinary developments of the ridge of the humerus indicates that the species is better able to dig in the ground than the others."

*Mus fossorius* is mentioned again twice in comparison with other species from Lagôa Santa, as follows.

(Page 280) "The first of these species [*i. e.* *Mus robustus* Lund =?, not *Hesperomys robustus* Burmeister = *Nectomys squamipes* Brants] is about the size of *Mus vulpinus* [= *Holochilus brasiliensis* Desmarest] but its form is more like that of *Mus principalis* [= *Kunsia tomentosus* Lichtenstein] and *M. fossorius*."

(Page 281) "*M[us] orycter* [= *Akodon nigrita* Lichtenstein] is a miniature *M. fossorius* from which it differs by its more delicate limbs."

Winge (1888:143) reviewed the Recent and Pleistocene mammals discovered by Lund in Minas Gerais. He regarded *fossorius* and all other rodents described from isolated humeri as indeterminable. PAULA COUTO (1950:271, footnote 285) suggests that *fossorius* may be *Nectomys squamipes* while AVILA PIRES (1960:39) treats *Mus fossorius* Lund, 1841, as a synonym of *Oxymycterus roberti* Thomas, 1901. If the latter is true, the name *fossorius* should replace *roberti*. However, it has not been demonstrated that *fossorius* and *roberti* are conspecific or even congeneric. LUND's description and comparisons of *Mus fossorius* indicate a very large cricetine such as *Nectomys squamipes*, a species of *Holochilus* or *Kunsia tomentosus*. The fossorial specialization and comparisons with *principalis* favor alignment of *fossorius* with *Kunsia*. Speculation aside, until the identity can be demonstrated by direct comparison, I accept WINGE's dictum and regard *Mus fossorius* Lund as indeterminable.

*Scapteromys labiosus* WINGE (1888:39, pl. 1, fig. 12 [head], fig. 13 [hind foot], pl. 3, fig. 1-1a [skull, molars]) should have been classified according to its author's own criteria as a *Habrothrix*, *i. e.*, genus *Akodon* of current taxonomy. Judged by the original description and figures of head, foot, skull and second upper molar, *labiosus* resembles *Akodon azarae* Fischer (= *arenicola* Waterhouse) with some fine but significant differences, notably in shorter and posteriorly wider incisive foramina, narrower mesopterygoid fossa and shallower concavity of posterior border of mandibular ramus. There is absolutely nothing about *labiosus* that suggests more than remote relationship to scapteromyines.

*Scapteromys modestus* Miranda Ribeiro (1914:29, pl. 20 [skin], figs. 5, 7 [skull]), judged from the published figure of its skull, is not a *Scapteromys*. Its author compared it with the obviously different *Scapteromys labiosus* Winge (vide supra), with *Mus musculus* Linnaeus and with *Oryzomys longicaudatus* Bennett. Its cranial and dental characters, insofar as they can be appreciated from the poor photographic reproductions, correspond to *Calomys callosus*. The same criteria were probably used by WINGE (1941:145) for identifying *modestus* with *Hesperomys expulsus* Lund (= *Calomys callosus expulsus*). However, if MIRANDA RIBEIRO's description is reliable, the external measurements of *modestus* with ear 11 mm. and tail slightly longer than head and body, depart slightly from those of *Calomys callosus*, while the whitish underparts and pollex with claw would exclude *Calomys callosus*.

### Metric Key to Genera of Scapteromyines

Size smaller, combined head and body length rarely more than 200 mm.; tail more than 68% of head and body length and provided with keel hairs and pencil; hind foot (with claw) more than 19% of head and body length; greatest skull length less than 45 mm.; alveolar length of molar row less than 8.0, width of  $m^1$  less than 2.5;  $m_1$  three rooted . . . . . *Scapteromys* (p. 99)

Size larger, combined head and body length rarely less than 200 mm.; tail less than 68% of head and body length and thinly haired throughout; hind foot (with claw) less than 20% of head and body length; greatest skull length more than 45 mm.; alveolar length of molar row more than 8.0 mm., width of  $m^1$  more than 2.5  $m_{13}$  four rooted . . . . . *Kunsia* (p. 112)

Note: The minimal linear dimensions for *Kunsia* are based on extrapolations from the measurements of a single skin and two fragmented skulls of *Kunsia fronto*. See Table 4 for actual measurements.

### Explanation of Map, figure 7

#### *Kunsia fronto chacoensis*

##### ARGENTINA

##### Chaco

Río de Oro, mouth at 27° S, 58° 35' W. A. Ros, September, 1896.

#### *Scapteromys tumidus* (1—34)

##### ARGENTINA

##### Chaco

1. Bermejo (Río), mouth at approximately 26° 50' S, 58° 21' W. Capt. J. PAGE.
2. Las Palmas, Riacho Ancho, 27° 08' S, 58° 41' W. Opposite Isla del Cerrito.

##### Entre Ríos

3. Médanos, 33° 27' S, 59° 08' W.
4. Sagastume (Arroyo), 33° 42' S, 58° 38' W. Ruta 12, km. 143.8.
4. Los Cisnes, Río Carabelas, 34° 00' S, 58° 50' W. Delta del Paraná, east of Campana. H. E. Box, Oct. 1919.

##### Buenos Aires

4. Pasaje Talavera, 33° 55' S, 59° 00' W. Delta del Paraná.
4. Isla Ella, not precisely located. Delta del Paraná. ROBIN KEMP, Jan. 1917.
4. Paraná Mini, not precisely located. At confluence with the Méndez Chico. Delta del Paraná. (Evidently not Río Paraná Mini, 27° 55' S, right bank Río Paraná).
4. Felipe (Arroyo), not precisely located. Delta del Paraná.

4. Isla Retama, not precisely located. Delta del Paraná.
5. Zárate, Arroyo Pesquerías, above Campana,  $34^{\circ} 09' S$ ,  $58^{\circ} 59' W$ .
6. Paraná de las Palmas,  $34^{\circ} 10' S$ ,  $58^{\circ} 58' W$ . At confluence with Canal 6.
7. Punta Lara (National Reserve),  $34^{\circ} 47' S$ ,  $58^{\circ} 01' W$ . E. MASSOIA, Dec. 1958; Jan., Oct. 1959; Jan., May, Sept. 1960. E. MASSOIA and FORNES, Jan. 1959. (For ecological data see RINGUELET, 1962, *Physis*, 23, (64):83—92).

## BRAZIL

## Río Grande do Sul

8. Porto Alegre,  $30^{\circ} 04' S$ ,  $51^{\circ} 11' W$ . R. HENSEL, before 1867.

## URUGUAY

## Artigas

9. Colonia Artigas (La Isleta), approximately  $30^{\circ} 45' S$ ,  $56^{\circ} 50' W$ . Not located, shown on map *fide* MASSOIA and FORNES (1964, fig. 5).

## Cerro Largo

10. Las Marías (Estancia),  $32^{\circ} 22' S$ ,  $54^{\circ} 11' W$ . 6 km. SE of Melo. J. C. BARLOW, Feb. 1963.

## Treinta y Tres

11. Tacuarí, mouth at  $32^{\circ} 46' S$ ,  $53^{\circ} 18' W$ . Collecting station 16 km. SSW. S. ANDERSON, J. C. BARLOW, March 1963; M. O. TUTTLE, A. XIMÉNEZ, April 1963.

## Durazno

12. Cañada del Sauce (Rincón de las Piedras),  $32^{\circ} 44' S$ ,  $56^{\circ} 05' W$ .

## Soriano

13. Soriano,  $33^{\circ} 24' S$ ,  $58^{\circ} 19' W$ . E. BUDIN, May 1924.
14. Estancia Arroyo Perdido, Santa Elena (See Mercedes).
14. Mercedes,  $33^{\circ} 16' S$ ,  $58^{\circ} 01' S$ .
15. Cardona,  $33^{\circ} 53' S$ ,  $57^{\circ} 23' W$ . Collecting station 3 km. E. M. D. TUTTLE, May 1963.

## Flores

16. Los Mirasoles, Cerro Colorado, approximately  $33^{\circ} 50' S$ ,  $57^{\circ} 00' W$ . Shown on map *fide* MASSOIA and FORNES (1964, fig. 5).
17. Arroyo Grande,  $33^{\circ} 58' S$ ,  $57^{\circ} 05' W$ . O. V. APLIN, between October 1892 — June 1893.

## Colonia

18. Artilleros,  $34^{\circ} 28' S$ ,  $57^{\circ} 33' W$ .
18. Santa Ana, Arroyo Artilleros (see Artilleros).
18. Santa Elena, Arroyo Artilleros (see Artilleros).
19. Colonia Valdense, La Paz,  $34^{\circ} 21' S$ ,  $57^{\circ} 18' W$ .

## San José

20. Santa Clara (Estancia) (see Chamizo).
20. Chamizo,  $34^{\circ} 10' S$ ,  $56^{\circ} 41' W$ .
21. San José,  $34^{\circ} 20' S$ ,  $56^{\circ} 42' W$ . R. VAZ-FERREIRA; E. MASSOIA at Ruta 1, km. 37.5.
22. Arazatí (Puerto),  $34^{\circ} 34' S$ ,  $57^{\circ} 00' W$ .
23. El Tigre, Delta,  $34^{\circ} 46' S$ ,  $56^{\circ} 33' W$ .
24. Santa Lucía, right bank, mouth at  $34^{\circ} 48' S$ ,  $56^{\circ} 22' W$ . A. LANGGUTH, Aug. 1963.

## Montevideo

25. Santa Lucía, left bank, mouth  $34^{\circ} 48' S$ ,  $56^{\circ} 21' W$ . S. ANDERSON, May 1963; J. C. BARLOW, April 1963.
26. Montevideo,  $34^{\circ} 53' S$ ,  $56^{\circ} 11' W$ . R. VAZ-FERREIRA.
26. Parque Lecoc, Montevideo (see Montevideo).

## Florida

27. Puntas del Arroyo Maciel (see Puntas de Maciel).
27. Puntas de Maciel,  $33^{\circ} 36' S$ ,  $56^{\circ} 21' W$ .

**Canelones**

28. Canelones,  $34^{\circ} 32' S$ ,  $56^{\circ} 17' W$ . Collected at Instituto Seroterápico. R. VAZ-FERREIRA, N. BRUN, July 1961.
29. Toledo (Arroyo), near Carrasco,  $34^{\circ} 49' S$ ,  $56^{\circ} 04' W$ .
30. Tropa Vieja (Arroyo)  $34^{\circ} 47' S$ ,  $55^{\circ} 48' W$ . Near Atlántida. A. LANGGUTH, Feb. 1963; E. MASSOIA and A. FORNES.
30. Salinas (Balneario),  $34^{\circ} 47' S$ ,  $55^{\circ} 51' W$ . SR. LARROSA, Nov. 1957.
30. Interbalneario, 36 km. E. of Montevideo,  $34^{\circ} 48' S$ ,  $55^{\circ} 51' W$ . J. C. BARLOW, M. D. TUTTLE, R. VAN GELDER, Dec. 1962.
30. Frasquito (Arroyo),  $34^{\circ} 44' S$ ,  $55^{\circ} 57' W$ . Tributary of lower Arroyo Pando.

**Maldonado**

31. Maldonado  $34^{\circ} 54' S$ ,  $54^{\circ} 57' W$ . C. DARWIN, June 1833; VAZ-FERREIRA.
32. Barra del Arroyo,  $34^{\circ} 54' S$ ,  $54^{\circ} 52' W$ . 9 km. ENE of Punta del Este.

**Rocha**

33. Lascano,  $33^{\circ} 40' S$ ,  $54^{\circ} 12' W$ . Collecting station, 22 km. SE. A. LANGGUTH, M. D. TUTTLE, May 1963.
34. Playa Solari,  $34^{\circ} 39' S$ ,  $54^{\circ} 11' W$ . West of La Palma.

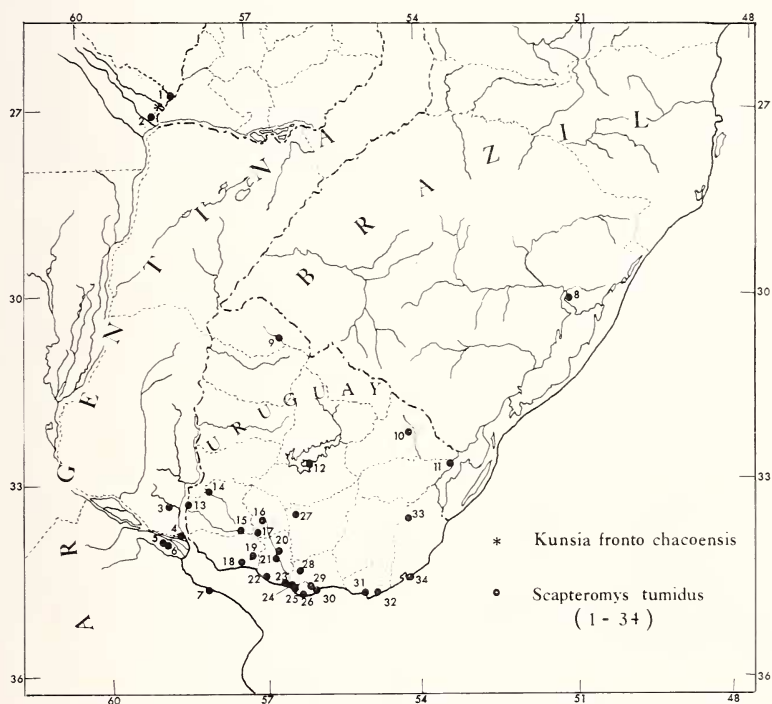


Fig. 7. Map, collecting localities of *Scapteromys tumidus* and *Kunsia fronto chacoensis*. See above for explanations.

### Genus *Scapteromys* Waterhouse

*Scapteromys* Waterhouse, 1837, Proc. Zool. Soc. London, 1837:20. GYLDENSTOLPE, 1932, Kungl. Sv. Vet. Akad. Handl., 11, (3):98 — characters; part species, *tumidus aquaticus*. ELLERMAN, 1943, Families and genera of living rodents, 2:8, 26, 330, 337, 425 — part, characters, classification. CABRERA, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia", 4, (2):474 — part, classification. HOOPER and MUSSER, 1964,



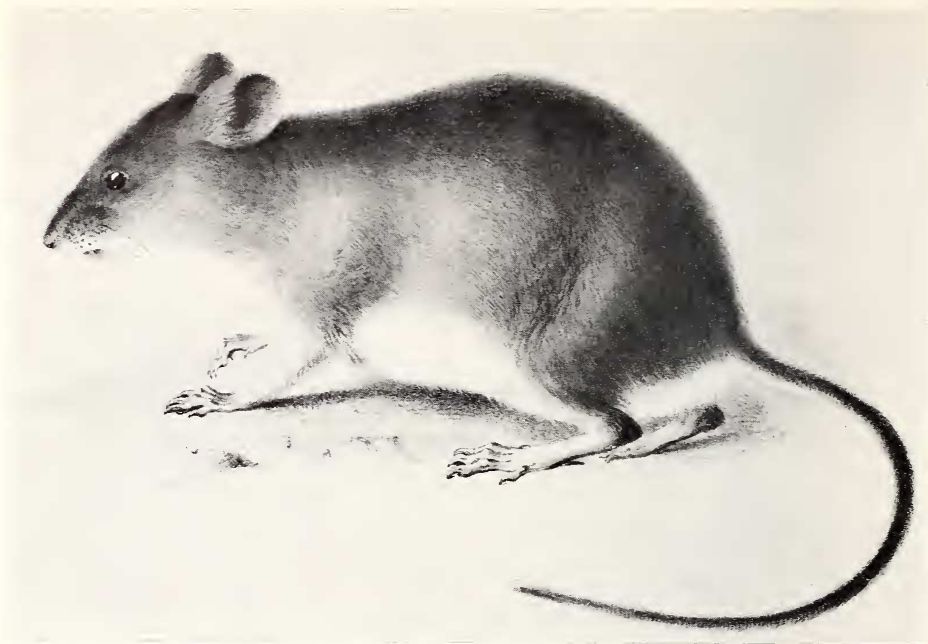


Plate 5. *Scapteromys tumidus* Waterhouse, type, reproduced from the original colored plate (about  $\frac{2}{3}$  natural size).

Misc. Publ. Univ. Michigan Mus. Zool., no. 123:29, 42, 53 — glans penis; classification. MASSOIA and FORNES, 1964, Physis, 24, (68):279 — taxonomy; distribution;

Type species. — *Mus (Scapteromys) tumidus* Waterhouse by original designation. Included species. — *Scapteromys tumidus* Waterhouse.

### Distribution

(Map, Figures 1, 7)

Shores of the Río de La Plata in Uruguay and Argentina to the coast of the Bahía de Samborombón, Buenos Aires Province, thence north along the Atlantic coastal swamps, lakes and lagoons of Uruguay into Río Grande do Sul, Brazil on the east, and on the west into the flood plains of the Río Uruguay and the Río Paraná-Paraguay in Uruguay, Argentina and, probably, extreme southwestern Paraguay.

### Characters

External. — Size moderate; external form adapted for palustrine and subaquatic life; pelage thick, soft, glossy; upper parts of head and body tawny to olivaceous more or less lined with black, sides of body less black, chest and belly more or less well defined gray washed with buffy to ochraceous sometimes with tawny patches, the dark gray bases of the thick pile not always concealed; lower sides of head like underparts; tail (fig. 2) well developed but not thick, the fine, stiff but not hispid pelage dark brown often becoming buffy to whitish terminally, three hairs to each scale, the scales fine and partially hidden; ventral keel hairs usually long, pencil present and always well defined, length of tail less pencil, approximately 85% (72%–99%) of combined head and body length; ears (fig. 3) comparatively small,



rounded, hairs of inner and outer surfaces like head and nape; forefoot (fig. 4) well developed but not markedly enlarged, vestigial pollex with sharp claw or clawlike nail, digits II–V strong, claws slender, slightly convex inferiorly each nearly as long as corresponding digit, plantar tubercles not notably specialized, digital bristles poorly developed or obsolete; hind foot (fig. 5) strong, elongate, length (with claw), approximately 24 % (21 %–28 %) of combined head and body length, claws slender, not markedly curved inferiorly, each slightly shorter than corresponding digit, narrow bands of interdigital webbing present between first phalanx of three middle digits and along inner border of each outer digit, digital bristles poorly to moderately developed, fifth postdigital plantar pad small or absent.

Cranial (pls. 11, 13–15). — Skull delicate the bones fine without crests or ridges; rostrum slender; nasals rounded distally, tapered proximally, generally to an attenuated point, and extending well behind fronto-maxillary sutures; anterodorsal frontal sinuses well inflated; zygomata strong but not heavy and deflected downward to level of alveoli; zygomatic plate strongly inclined laterally and widely separated from preorbital foramen in front; postorbital process absent; arc formed by frontoparietal suture less than semicircular; median parietal suture more than one-half as long as median frontal suture; hamular processes of squamosal (temporal) slender and dividing temporal vacuity into conspicuous dorsal and ventral segments; occipital more or less rounded with lateral and median inflations, the median crest undeveloped; mastoidal capsule (petrosal) visibly inflated; mandibular ramus comparatively weak and elongate, height less than one-half greatest length of mandible without incisor; capsular projection at base of coronoid process not forming a tubercular process.

Dental (fig. 6; pls. 17, 19). — Incisors without notable specialization but color of outer surface of lower dilute; occlusal surface of unworn molars slightly terraced; general outline of unworn to moderately worn upper and lower first two molars E-shaped, of lower third molars E- to S-shaped;  $m^2$  longer than wide; lower first molar with 3 roots; upper anterior median fold present and persistent in moderately worn  $m^1$ ; marginal opening of primary folds of first two upper and lower molars usually persistent in moderately worn teeth; second secondary fold persistent in unworn to slightly worn upper molars, obsolete or absent in lowers; paralophule-mesostyle (= pseudomesoloph) usually discrete and distinguished from paracone by a distinct fold; entolophulid weak and fused with mesolophid; vestigial mesoloph rarely discrete or persistent in  $m^1$  or  $m^2$ , mesolophid usually present and well developed in  $m_{1-2}$ , absent in  $m_3$ , rudimentary ectolophid sometimes present in unworn molars, absent in worn; worn  $m^3$  simple, usually cylindrical with vestige of coalesced second folds and first internal fold persisting as a single enamel island, unworn  $m^3$  with vestigial mesoloph and paralophule often present, first and second primary folds and first secondary folds shallow but well defined and open to the margin, first internal fold large and deep, second internal fold sometimes defined.

Phallic. — Male phallic characters are described elsewhere (p. 131, figs. (10–13).

### *Scapteromys tumidus* Waterhouse (fig. 8; pl. 5)

*Mus tumidus* Waterhouse, 1837, Proc. Zool. Soc. London, 1837:15. WATERHOUSE, 1839, Zool. Voy. "Beagle", p. 57, pl. 18 (animal), pl. 34, fig. 11a (lower molars) — Uruguay: Maldonado.

*Mus (Scapteromys) tumidus* Waterhouse, 1837, Proc. Zool. Soc. London, 1837:21 — classification; type of *Scapteromys*.

*Hesperomys tumidus* Hensel, 1873, Abh. Akad. Wiss. Berlin, 1872:46, pl. 3, figs. 20, 30 (molars) — Brazil: Rio Grande do Sul (Porto Alegre); 3 juvenals in spirits, Berlin Museum. FIGUEIRA, 1894, Anal. Mus. Nac. Montevideo, 2:17 (separate) — Uruguay.

- H[esperomys (Scapteromys)] tumidus* Thomas, 1884, Proc. Zool. Soc. London, 1884:449 — classification.
- Hesperomys (Scapteromys) tumidus* Ihering, 1892, Mammíferos do Rio Grande do Sul, p. 109 — Brazil: Rio Grande do Sul.
- Scapteromys (Hesperomys) tumidus* Aplin, 1894, Proc. Zool. Soc. London, 1894:308 — Uruguay: (Arroyo Grande); type, "an immature and much faded skin", ex THOMAS in litt.
- Scapteromys tumidus* Trouessart, 1897, Cat. Mamm., p. 534 — classification.
- S[capteromys] tumidus* Thomas, 1917, Ann. Mag. Nat. Hist., (8), 20:96 — Uruguay: SORIANO; MALDONADO; type skin with imperfect skull.
- Scapteromys tumidus* Sanborn, 1929, Field Mus. Nat. Hist., Zool. Ser., 17:158 — Uruguay: GYLDENSTOLPE, 1932, Königl. Sv. Vet. Akad. Handl., 11, (3):98, pl. 11, fig. 3 (skull), pl. 18, fig. 4 (molars) — Uruguay: (Soriano). YEPES, 1938, Rev. Centro Estud., Buenos Aires, 2:16 (separate) — Argentina: Entre Ríos (delta del Paraná). LEGRAND, 1960, Anal. Mus. Hist. Nat., Montevideo, (2) 6, (7):53 — Uruguay: Montevideo (Carrasco); ecology of Carrasco; common name, *rata de bañado*. HOOPER and MUSSER, 1964, Misc. Publ. Univ. Michigan Mus. Zool. no. 123:6, 22, 29, 30, 42, 49 — Uruguay: Canelones; glans penis; classifications.
- S[capteromys] tumidus tumidus* Massoia and Fornes, 1963, Physis, 24, (67):239 — Uruguay: Artigas; Colonia; Soriano; Flores; Durazno; Florida; Montevideo; Canelones; Maldonado; San José; Rocha.
- Scapteromys tumidus tumidus* Massoia and Fornes 1964, Physis, 24, (68):285, figs. pp. 282, 283, 285 (skull), fig. p. 288 (animal), fig. p. 293 (hand, foot, bacula) — Uruguay: San José (Chamizo; Pto. de Arazaté; San José; Delta El Tigre); Rocha (Playa Solari); Soriano (Santa Elena); Colonia (Santa Ana; Santa Elena; La Paz); Flores (Cerro Colorado); Durazno (Cañada del Sauce); Florida (Puntas de Maciel); Artigas (Colonia Artigas); Maldonado (Barra del Arroyo Maldonado); Canelones (Tropa Vieja; Arroyo Toledo; Arroyo Salinas; Arroyo Frasquito); Montevideo (Parque Lecoq); characters; comparisons; distribution; taxonomy; habits.
- Scapteromys aquaticus* Thomas, 1920, Ann. Mag. Nat. Hist., (9), 5:477 — Argentina: Buenos Aires (type locality, Isla Ella, delta Río Paraná); Entre Ríos (Los Cisnes, Río Carabelas); type, male, skin and skull, British Museum (Natural History) no 17.6.1.6, collected 15 February, 1917, by R. KEMP, YEPES, 1938, Rev. Centro Estud., Buenos Aires, 2:16 (separate) — Argentina: MASSOIA, 1961, Publ. Mus. Municipal Cienc. Nat. Trad., Mar del Plata, 1, (4):122, figs. 3, 13 (skull), fig. 15 (upper molars) — Argentina: Buenos Aires (Punta Lara, Río de la Plata); measurements; habits. HOOPER and MUSSER, 1964, Misc. Publ. Univ. Michigan Mus. Zool., no. 123:6, 8, 10, 22, 29, 30, 42, 49, fig. 7 a—c (glans penis) — Argentina: Buenos Aires; characters of glans penis.
- S[capteromys] tumidus aquaticus* Massoia and Fornes, 1963, Physis, 24, (67):239 — Argentina: Chaco (Las Palmas; Riacho Ancho); Entre Ríos (Arroyo Sagastume; Médanos); Buenos Aires (Punta Lara; Zárate; Delta del Paraná).
- Scapteromys tumidus aquaticus* Massoia and Fornes, 1964, Physis, 24, (68):289, figs. pp. 282, 283, 285 (skulls), fig. 4, lower (animal), fig. 6 (animal, tail, hand, foot, bacula) — Argentina: Buenos Aires (Punta Lara; Zárate; Pasaje Talavera; Paraná Mini; Arroyo Felipe; Isla Ella; Isla Retama; Paraná de Las Palmas); Entre Ríos (Arroyo Sagastume; Médanos); Chaco (Las Palmas); characters; comparisons; distribution; taxonomy; habits.
- Scapteromys tomentosus* Thomas (not Lichtenstein), 1917, Ann. Mag. Nat. Hist., (8), 20:96 — Argentina: Buenos Aires (Isla Ella, delta del Río Paraná); regarded as a blackish delta representative of *tumidus*. VAZ-FERREIRA, 1960, Arch. Soc. Biol. Montevideo, 24:67 — Uruguay: Soriano; San José; Canelones; Montevideo; Maldonado; in "bañados".
- Scapteromys tomentosus* Sanborn (not Lichtenstein), 1929, Field Mus. Nat. Hist., Zool. Ser., 17:158 — listed.
- Sc[apteromys] tomentosus* Yepes (not Lichtenstein), 1935, Rev. Inst. Bacteriol. Buenos Aires, 7 (2):234 — Argentina: Entre Ríos.
- Type. — Female, skin and skull, British Museum (Natural History) no. 55.12.24.18; collected June 1833 by CHARLES DARWIN.



Fig 8. *Scapteromys tumidus*, from a posed spirit preserved specimen (about  $\frac{1}{3}$  natural size).

Type locality. — Maldonado, southeastern corner of Uruguay.

Distribution. — As for the genus.

Characters. — Those of the genus.

Measurements. — See Table 4, page 108.

### Taxonomy

*Scapteromys aquaticus* Thomas from Isla Ella is based on one of 15 specimens collected in the Delta del Paraná by ROBIN KEMP in 1917. The series was first misidentified by THOMAS (1917:96) as *Scapteromys tomentosus* Lichtenstein with the observation that it differed only in tone of color from the type of *S. tumidus* and a referred specimen from Soriano. Later, when THOMAS (1920:477) proposed the name *Scapteromys aquaticus* for the Delta specimens, he compared them only with the published description of *tomentosus*. With five of the original Isla Ella series of *aquaticus* and three Soriano, Uruguay specimens identified by THOMAS as *tumidus* before me, I cannot detect any basis for distinguishing *aquaticus* as more than a very slightly differentiated population of *tumidus*.

MASSOIA and FORNES (1964:282) compared 103 Uruguayan with 156 Argentine representatives of *Scapteromys* and found no significant differences between them or their habitats. Nevertheless, swamp rats of the north bank of the Paraná in Uruguay were nominally distinguished as *S. t. tumidus* Waterhouse, and those of the south bank, in Argentina, as *S. t. aquaticus*. MASSOIA and FORNES separated the first from the second by smaller size, less weight, darker color, U- or V- rather than W-shaped fronto-parietal suture and wider mesopterygoid fossa. The smaller size of Argentine populations is not evident in our material and the darker color appears to be clinal with the darkest population from Punta Lara, Buenos Aires, at the southeastern extreme of the range. Sutural outlines and width of mesopterygoid fossa are individual variables (cf. p. 105, beyond). Measurements in millimeters of overall size of animal and width of mesopterygoid fossa given by MASSOIA and FORNES (1964:286, 290) for *tumidus* and *aquaticus* are compared in Table 1 for each sex with means followed by extremes in parentheses, and number of specimens.

Table 1

Measurements of "*S. t. tumidus*" and "*S. t. aquaticus*" from MASSOIA and FORNES (1964:286, 290).

Specimens of *tumidus* from 6 localities in the departments of San José, Montevideo and Canelones, Uruguay; *aquaticus* from Punta Lara, Buenos Aires, Argentina.

Character	Males Means, extremes, no. of specimens	Females Means, extremes, no. of specimens
<i>Greatest length</i>		
<i>tumidus</i>	323.0(300—353)16	316.0(300—336)9
<i>aquaticus</i>	323.7(310—340)36	314.1(290—340)26
<i>Head and body</i>		
<i>tumidus</i>	173.0(152—188)16	175.2(160—185)9
<i>aquaticus</i>	180.7(160—198)36	170.0(152—190)26
<i>Skull length</i>		
<i>tumidus</i>	40.1(39.3—42.9)15	40.7(39.5—42.3)9
<i>aquaticus</i>	40.1(39.0—41.1)21	39.2(38.0—40.7)21
<i>Mesopterygoid fossa, width</i>		
<i>tumidus</i>	2.1(1.7—2.5)16	2.0(1.8—2.2)11
<i>aquaticus</i>	2.2(1.8—2.5)31	2.2(1.8—2.5)24

## Variation

Size. — There is no significant geographic variation in size. However, local populations or pockets of swamp rats sometimes differ markedly from each other in mean size or proportions of parts. Table 2 shows variation in relative length of tail and hind foot in adults and juvenals of some local populations of *Scapteromys tumidus*. Size of hind foot seems to be more stable than tail length but one point in relative hind foot length is equivalent to approximately four points in relative tail length. In either character, individual variation is greater than the mean differences between populations. Differences between the sexes are not apparent and their measurements may be combined for greater accuracy. As in virtually all mammals, hind foot length

Table 2

Variation in relative length of tail and hind foot in several populations  
of *Scapteromys tumidus*

The means are followed by the extremes, in parentheses, and the total number of samples; see table 4 for actual measurements.

Locality	Tail Head and Body	Hind Foot Head and Body
ARGENTINA		
Punta Lara, Buenos Aires	86(81—95)5 ♂♂ ♀♀	23(22—25)5 ♂♂ ♀♀
Delta Paraná, Buenos Aires	86(82—92)8 ♂♂ ♀♀	24(23—26)7 ♂♂ ♀♀
URUGUAY		
Cardona, Soriano	89(76—99)13 ♂♂	24(21—28)13 ♂♂
	90(83—97)12 ♀♀	24(22—26)12 ♀♀
	93(89—97)7 Juv.	28(24—31)7 Juv.
Interbalneario, Canelones	81(75—87)4 ♂♂	23(24—26)4 ♂♂
	81(74—91)9 ♀♀	23(21—27)8 ♀♀
	88(83—99)5 Juv.	29(27—31)5 Juv.
Barra del Arroyo, Canelones	79(72—89)7 ♂♂	24(21—26)7 ♂♂
	80(78—82)5 ♀♀	24(23—25)5 ♀♀
Río Tacuari, Treinta y Tres	90(84—96)8 ♂♂	22(20—24)8 ♂♂
	90(75—97)9 ♀♀	24(21—26)9 ♀♀
Santa Lucía, Montevideo	87(80—99)5 ♂♂ ♀♀	25(22—28)5 ♂♂ ♀♀

of juvenals is relatively greater than in adults. Tail is also relatively longer in juvenals than in adults of species where the ratio of tail length to combined head and body length is less than 100:100.

Color. Color differences between populations are slight and fully intergrading. Younger individuals are generally darker than older ones. The trend from coast inland or, roughly from south to north, is toward increase in intensity of ochraceous suffusion on underparts with its corresponding reflection on sides of body. Underparts in darkest series from Punta Lara, Buenos Aires, at southern extreme of the range, are dominantly gray and sharply defined from sides, upper parts heavily overlaid with blackish. Delta material (including 5 topotypes of *aquaticus*) is slightly paler throughout with more buff or ochraceous on underparts; chin to chest and under-surface of arms in one specimen of the original series of *aquaticus* are tawny, the belly with some irregular tawny streaks and flecks; chin to belly in a second topotype sparsely streaked and flecked with tawny. Specimens from coastal localities in departments of San José, Montevideo and Canelones are slightly more uniformly pale on under-



parts, more buffy on sides. Maldonado populations are similar. Northward, in Rochas, Treinta y Tres, Cerro Largo and Soriano, underparts are dominantly ochraceous buff and least defined from sides. Underparts of a lone specimen from Río Bermejo, Argentina, at northwestern extreme of range are creamy buff and sharply defined from pale brown of sides and upper parts which appear to be discolored from liquid preservative. Tail varies individually. It is uniformly dark brown or with keel and pencil variably mixed with gray to ochraceous the paler hairs usually concentrated on proximal portion; sometimes entire ventral surface is gray, ochraceous or tawny. Upper surface of hind feet are thinly covered with gray or pale brown hairs or mixture of both; digital bristles silvery. Ears are colored like dorsal surface.

**Cranial and dental.** — Geographic and local variation is not evident. Individual variation among adults is partly reflected in cranial measurements (Table 4) and proportions. The usual variables in suture outline, position and number of most foramina, degree of convexity of dorsal cranial plane, etc. are as much individual as ontogenetic. Mean width of mesopterygoid fossa regarded as a subspecific character by Massoia and Fornes varies the same in both sexes and all localities in our material. Juvenals are distinguished primarily by the proportionately larger braincase and wider supraorbital region, shorter muzzle, finer incisors but disproportionately larger and unworn molars. In three of four fully adults from Punta Lara, Buenos Aires, received in exchange from the Museo de La Plata, the molars are degenerate or lost, their alveoli distorted from diseases. The condition is characteristic of cage reared animals but the skin tag data indicate that the three animals were wild caught September 1960, July 1961, May 1962, respectively, by E. MASSOIA. Altogether, 120 Punta Lara specimens were examined by MASSOIA and FORNES (1964:289) but dental abnormalities are not mentioned.

**Sexual.** — The sexes are indistinguishable except by the usual organic differences.

**Phallic.** — See p. 131 for description of male phallic characters.

### Habits and Habitat

"This rat was caught in so wet a place among the flags bordering a lake, that it certainly must be partly aquatic in its habits", wrote CHARLES DARWIN (in WATERHOUSE, 1839:58) of the type specimen collected near Maldonado. *Scapteromys tumidus* is indeed the *rata de bañado*, or swamp rat of Uruguay and northeastern Argentina.

The islands of the Paraná Delta in Buenos Aires, Argentina, where the original series of *Scapteromys aquaticus* was obtained, are described by the collector, ROBIN KEMP (in THOMAS, 1917:95) as "remarkable for the fact that they are more less completely flooded when a south-east wind banks up the waters of the La Plata Estuary, and Mr. KEMP records that he has had to wade through the rising waters to retrieve his traps, and that then, the water having fallen and the traps been re-set, he has again caught numbers of specimens. This shows, of course, that all the local species have learnt to take refuge in trees, unless they are themselves absolutely aquatic. That such animals are *Oryzomys*, *Oxymycterus*, *Akodon* and the new genus *Deltamys*, all normally terrestrial, should thus have become arboreal on occasion, is a remarkable case of adaptation to local conditions." Mr. KEMP has noted on the labels of his specimens of *Scapteromys* that they were collected in orchards bordering ponds and in "osier beds" and "withy beds".

According to the Argentine mammalogist ELIO MASSOIA (1961:124) the swamp rats of Punta Lara, Río del Paraná, below Buenos Aires, live only in flood plains thickly covered with sedge particularly the cutting sedge (*Cortaderia*) and false cutting grass (*Scirpus giganteus*). MASSOIA notes that *Scapteromys* is nocturnal and

crepuscular and is a good swimmer. Stomachs he examined contained segments of earthworms and insect larvae. The stomach of one preserved specimen at hand, (AMNH 206211) from east of Arroyo Pando, Canelones, Uruguay, examined for insects by my colleague, Dr. RUPERT WENZEL, contained a pulpy mass of plant tissue, a fly wing and a fly pupa.

In their definitive monograph of *Scapteromys*, MASSOIA and FORNES (1964:293-295) give a more detailed account of the habits of swamp rats observed in Punta Lara and the Delta region in Buenos Aires Province, Argentina. The following is a free translation from the Spanish of their observations.

"The swamp rat is omnivorous but *rutilans* prefers earthworms. Presumably this puts it into competition with sympatric *Oxymycterus rutilans*. Both species search out and devour earthworms in much the same way. *Scapteromys* detects its prey by smell then traps it by rooting and digging. Once the earthworm is exposed, the rat seizes and immobilizes it by gashing the whole length of the worm's body with its incisors. The worm is then bitten into segments each of which is grasped by the rat, chewed thoroughly and noisily and quickly swallowed.

"The fossorial proclivities of *Scapteromys* may have been exaggerated by previous observers. Although its claws are long and stout we believe they are primarily adapted for securing food. We have never seen wild or captive *Scapteromys* excavating galleries. They may dig small holes for nesting under the vegetation but one lactating female we found was nesting on the ground hidden only by a thick cover of vegetation.

"The sounds made by an excited swamp rat are quite different from those uttered by *Rattus*. Suckling young emit a very high pitched 'chi-chi' or 'chio-chio'. The adult vocalization is pitched lower. Two adult captives uttered a slow 'ro-ro-ro' which was not unlike the call of the wren known locally as *ratona* or *tacuarita* (*Troglodytes musculus*). This sound, however, becomes a shrill 'cree-cree' when the rat is excited or harassed and it may rise to a higher and sustained 'cree . . . ec' if the animal should be cornered and in pain."

"The swamp rat is a good climber. Its scansorial ability combined with natatorial skill permit *Scapteromys* to live on flood plains where tall plants provide a haven from floods. The long claws and flexible tail are particularly useful in climbing. A captive was observed to leap up and hook its claws into the mesh of the walls of its cage in the same fashion as the small long tailed scansorial *Oryzomys flavescens* and *O. delticola*. *Scapteromys* is a nimble runner. It is semi-plantigrade like *Akodon azarae* [= *A. agreste* Brants, 1827, Het Geschl. Muiz, p. 184] and more quadrupedal than *Calomys*. The latter frequently jumps or runs on its hind legs only and often stands erect on the tips of its hind toes. *Scapteromys*, on the other hand, keeps tail and hind legs on the ground even when grooming or feeding.

"*Scapteromys* dives readily and swims easily and swiftly. In swimming, only its head and anterior portion of the back are exposed as in other aquatic rodents such as *Holochilus* ('rata nutria') and *Myocastor* ('quiya' or 'nutria'). The rat propels itself by horizontal undulations of the tail, rowing movements of the hind feet and short paddling motions of the fore feet. The fur remains nearly completely dry during immersion. Evidently, the pelage is annointed with a waterproofing substance secreted by the skin. In contrast, we have never seen *Oxymycterus* take to water unless driven to it in self defense and its pelage, once immersed, becomes completely soaked. The swamp rat is an attractive animal in captivity. It seems to tame easily but remains shy. It does not hesitate to bite when seized and is cannibalistic, at least in captivity.

"*Scapteromys* has a highly developed sense of hearing and can perceive sounds of extremely high wave lengths. It is easily startled and seeks safety by plunging into the nearest body of water. Its vision is good but we were never able to shine its eyes even with a 500 watt lamp."



MASSOIA and FORNES found *Scapteromys tumidus* sharing habitats with the cricetine *Akodon agrestes* (= *azarae*), *Calomys laucha*, *Oxymycterus rutilans*, *Holochilus brasiliensis*, *Oryzomys delticola*, *Oryzomys flavescens* and *Akodon kempfi*.

### Reproduction

Breeding data for *Scapteromys tumidus* recorded on the individual skin tags of specimens collected from December 1962 through May 1963, by the American Museum of Natural History zoological expedition in Uruguay, are summarized in Table 3, below.

Table 3  
*Scapteromys tumidus*, breeding data

Month	Locality	Total specimens	♂♂ Juv.	Adult testes length in mm.	♀♀ Juv.	Number of embryos				
						0	1	2	3	4
December	36 km. E. Montevideo	5 ♂♂, 14♀♀	1	11, 14, 18	5	1 <sup>1</sup>			1	4
February	Melo	2 ♂♂	0	12, 14	0					
	Tropa Vieja	1♀	0	—	0	1				
March	Río Tacuari	1 ♂, 1♀	0	13	0	1				
April	Río Tacuari	8 ♂♂, 10♀♀	0	11, 14, 14, 14, 15	0	3				
	Sta. Lucia	1 ♂♂, 4♀♀	0	13	1	3				
May	Sta. Lucia	1 ♂, 1♀	0	10, 5	0					
	Barra del Arroyo	7 ♂♂, 9♀♀	0	10, 10, 12, 15	3	1				
	Cardona	20 ♂♂, 18♀♀	3	(8–16 mm.) 13 specimens	4	11			1	1

<sup>1</sup> Vertical column shows the number of females for each number of embryos listed in the horizontal column above.

The meager data shows breeding high in December during the early summer rainy season, followed by a decline with a low in April and May. Two to four young may be produced in a litter. MASSOIA and FORNES (1964:264) made similar findings. They noted gravid females in January and November but none with full term fetuses. In late January they found one suckling young about a week old with eyes still closed, and a female with two well developed fetuses which would have come to term in February. Information for other months of the year is not given. The authors add that the number of fetuses per female varies from two to four.

Present data indicates that the reproductive cycle in *Scapteromys* agrees with that of other southern hemisphere cricetines, e. g., *Phyllotis* sp. (cf. HERSHKOVITZ, 1962: 278, 449). Judged by the number of fetuses, the number of litter young in *Scapteromys* is low for cricetines in general.

### Specimens examined

TOTAL: 116. Argentina: Buenos Aires: Isla Ella, 5 (BM, 4; CNHM, 1); Punta Lara, 5 (BM, 1; CNHM, 4); Chaco: Río Bermejo, 1 (USNM); Entre Ríos: Los Cisnes, 2 (BM); Uruguay: Canelones: Arroyo Tropa Vieja, 36 km. E. of Montevideo, 1 (AMNH); Balneario, Salinas, 1 (CNHM); Canelones, 1 (CNHM); Interbalneario, 36 km. E. of Montevideo, 18 (AMNH); Cerro Largo: Estancia Las Marías, 2 (AMNH); Maldonado: Barra del Arroyo, 14 (AMNH); Montevideo: Bañados de Carrasco, 1 (CNHM); Montevideo, 1 (BM); Río Santa Lucía, 1 km. S. E. of Santiago Vasquez, 7 (AMNH); Rocha: Lascano, 22 km. S. E., 2 (AMNH); San José: Río Santa Lucía, 2 (CNHM); Soriano: Cardona, 3 km. E., 32 (AMNH); Soriano, 3 (BM); Treinta y Tres: Río Tacuari, Boca, 16 km. S. S. W., 18 (AMNH).

Table 4  
*Scapteromys tumidus* Waterhouse, measurements in millimeters

Locality	Head and Body	Tail	Hind Foot <sup>1</sup>	Ear	Weight	Skull Greatest Length	Condyllo-basal Length	Zygomatic Breadth
URUGUAY								
Canelones 36 km.			36(33-39)13					
E. Montevideo	173(145-194)13	139(123-155)13	40(38-42)13	24(22-28)13	128(72-175)13	39.3(35.7-41.7)11	37.1(33.7-39.5)11	19.4(17.7-20.6)13
Canelones	180	165	37 38	25		42.3	40.0	21.1
Maldonado			37(35-40)12					
Barra d. Arroyo	174(150-197)12	139(121-150)12	41(38-43)12	25(20-29)12	142(93-165)12	39.6(35.8-41.4)11	37.6(33.8-39.5)11	19.9(18.2-21.0)11
Montevideo			36(34-37)6					
Rio Santa Lucía	166(143-185)6	141(132-154)5	40(38-41)6	25(23-28)6	133(90-168)6	39.1(37.0-41.5)5	37.2(34.5-39.3)5	19.6(18.3-21.2)5
Montevideo	170	140	—	24	—	40.1	38.6	19.7
Rocha			35, 38					
Lascano	157, 199	151, 158	39, 43	23, 26	132, 195	—, 43.8	—, 42.1	19.6, 21.1
San José			36, 36					
R. Santa Lucía	167, 171	143, 139	40, 40	22, 22	115, 110	39.2, —	37.3, —	18.8, 20.3
Soriano			36(28-39)14					
Cardona ♂ ♂	165(107-188)14	148(99-168)14	40(31-42)14	24(19-26)14	—	38.9(35.2-41.4)10	37.2(33.4-39.5)10	19.7(17.7-20.9)12
Cardona ♀ ♀	164(137-188)12	148(128-157)12	36(35-37)12	24(22-27)12	—	39.0(35.2-41.0)11	37.2(33.5-40.0)11	19.5(17.8-21.3)13
Treinta y Tres			40(38-41)12					
Rio Tacuarí	172(152-191)17	153(134-164)17	36(35-39)17	24(21-28)16	124(86-159)18	39.9(38.6-41.2)8	37.9(36.7-39.3)8	19.6(18.3-21.1)12
ARGENTINA								
Buenos Aires			40(38-42)17					
Isla Ella <sup>2</sup>	168	154	36 —	22.5	—	39	37	19
Isla Ella	155, 158, 163	127, 146, 139	35, 34, 36 <sup>3</sup> 38, 38, 39	21, 22, 23	—	38.3, 38.3, 39.2	36.3, 36.5, 37.6	—, 19.2, 18.9
Punta Lara	165, 173, 185	146, 144, 150	35, 35, 36 <sup>3</sup> 39, 38, 40	23, 22, 24	—	39.7, 40.3, 40.4	38.5, 38.3, 39.3	18.9, 19.6, 20.9
Entre Ríos			33, 36 <sup>3</sup>					
Los Cisnes	151, 150	124, 125	36, 38	21, 20	—	—	35.1, 36.6	18.4, 18.6

Locality	Interorbital Constriction	Braincase width	Nasals	Incisive Foramina	Diastema	Zygomatic Plate	Alveolar length of molar row	m <sup>1</sup> -width
<b>URUGUAY</b>								
Canelones								
36 km.								
E. Montevideo	5.7(5.4-5.9)13 5.8	15.9(15.4-16.4)11 16.7	15.4(13.4-16.9)13 17.8	8.9(7.9-9.4)13 9.6	9.7(8.0-10.8)13 10.6	3.7(3.1-4.2)13 4.0	7.1(6.7-7.4)13 7.2	2.3(1.9-2.3)13 2.0
Canelones								
Maldonado								
Barra d. Arroyo	5.7(5.4-6.1)13	16.0(16.4-16.5)11	15.3(13.7-16.1)13	8.7(7.4-9.6)13	9.8(8.4-10.6)13	4.0(3.1-4.4)13	7.0(6.5-7.6)13	2.2(2.2-2.3)10
Montevideo								
Río Santa Lucía	5.7(5.4-6.0)6 5.7	16.2(15.9-16.7)5 16.4	15.7(14.6-17.1)6 16.0	8.6(8.1-9.0)6 8.7	9.7(8.5-10.8)6 10.2	3.8(3.5-4.0)6 3.9	7.0(6.8-7.4)6 7.4	2.1(1.9-2.2)6 2.1
Montevideo								
Rodha								
Lascano	5.8, 5.9	—, 16.4	15.7 17.5	8.9, 9.9	9.9, 11.1	3.4 4.4	6.9, 7.7	2.1, 2.2
San José								
R. Santa Lucía	5.9, 5.6	16.5, 16.1	16.5, 14.7	8.4, 8.3	10.1, 10.8	4.0, 3.9	6.8, 7.0	2.3, 2.3
Soriano								
Cardona ♂	5.7(5.5-6.1)16	16.5(15.7-17.4)12	15.4(13.7-16.8)13	8.9(7.5-9.7)16	9.6(8.3-10.9)16	3.8(3.3-4.3)16	7.1(6.8-7.7)16	2.1(1.9-2.3)14
Cardona ♀	5.7(5.4-6.1)13	16.3(15.6-16.7)11	15.6(13.6-17.1)13	9.0(8.0-10.0)13	9.8(8.3-11.3)13	3.8(3.5-4.2)13	7.0(6.7-7.5)13	2.2(2.1-2.4)12
Treinta y Tres								
Río Tacuareí	5.7(5.3-6.0)16	16.1(15.4-16.6)9	15.9(14.5-16.7)15	8.8(8.1-9.4)15	9.7(9.1-10.6)15	3.8(3.4-4.2)16	7.2(6.7-7.8)17	2.0(1.8-2.2)15
<b>ARGENTINA</b>								
Buenos Aires								
Isla Ella <sup>1</sup>	6	16	15	8	—	3.7	6.4 <sup>4</sup>	—
Isla Ella	6.0, 6.0, 6.1	15.6, 15.5, 16.3	15.1, 14.6, 15.0	8.0, 8.1, 8.5	9.9, 10.2, 10.3	3.5, 3.4, 3.6	6.8, 6.6, 6.6	2.1, 2.2, 2.2
Punta Lara	5.9, 6.1, 6.0	15.9, 16.3, 16.8	15.7, 15.6, 16.2	8.8, 8.4, 9.3	10.0, 9.6, 10.3	3.6, 4.0, 4.1	—	2.1, —, 2.3
Entre Ríos								
Los Cisnes	5.9, 5.8	15.3, 16.1	14.1, 14.2	7.6, 8.2	9.0, 10.1	3.6, 3.4	6.9, 6.1	2.1, 1.9

<sup>1</sup> Without claw/with claw. — <sup>2</sup> Type of *aquaticus* Thomas from original description. — <sup>3</sup> Measured on dry skin. — <sup>4</sup> Crown length.

Table 5  
Kunsia, measurements of the species, in millimeters

Locality	Head and Body	Tail	Hind foot <sup>1</sup>	Ear	Skull Greatest length	Condylar-basal length	Zygomatic breadth	Interorbital Constriction
<i>tomentosus</i>								
BRAZIL								
Rio Uruguay, <sup>2</sup>	287, 270	157, 150 +	52 <sup>3</sup> , 41/45	33,—	—	—	—	—
Lagôa Santa <sup>4</sup>	—	—	—	—	—	—	—	8.0, 8.25
Campos Novos <sup>6</sup>	267	160	—	—	55	—	—	—
Chapada <sup>7</sup>	—	—	—	—	—	ca. 40.4	24,5	8.4
BOLIVIA								
San Joaquín	252, 260	150, 140	40 <sup>8</sup> , 43 <sup>8</sup> 46 49	32,31	52.5, 52.2	52.2, 51.7	ca. 31.4, 29.4	9.0, 9.2
<i>dhacoensis</i>								
ARGENTINA								
Río de Oro <sup>9</sup>	225	110	38/43 <sup>8</sup>	—	—	—	24.1	6.7
BRAZIL								
Lagôa Santa <sup>10</sup>	—	—	—	—	—	—	—	7.0

<sup>1</sup> Hind foot measurements given are without claw / with claw. — <sup>2</sup> Type of skin and skull of *tomentosus* Lichtenstein; first set of external measurements from original description with old German indices converted to millimeters, second set from dry skin; cranial measurements from fragmented skull. — <sup>3</sup> Evidently incorrect. — <sup>4</sup> Type skull of *principalis* Lund ex WINGE (1888, E. Mus. Lundii, 1 [3]:42, pl. 3, fig. 2 [skull]); followed by measurements of a juvenile cotype with m<sup>3</sup> eruptive. — <sup>5</sup> Measurement from original figure of type skull. —

Locality	Braincase Width	Nasals	Incisive foramina	Diastema	Zygomatic Plate	Alveolar length of molar row	m <sup>1</sup> -width
<i>tomentosus</i>							
BRAZIL							
Rio Uruguay <sup>2</sup>	19.3	—	—	—	—	10.5	3.4
Lagôa Santa <sup>4</sup>			12.3, 9.5	14.0, 11.7	6.4 <sup>5</sup> × 10.3, — × 8.0	11.3, 10.0	
Campos Novos <sup>6</sup>							
Chapada <sup>7</sup>	—	13.7	9.1	9.9	4.8 × —	10.3	3.4
BOLIVIA							
San Joaquín	19.7, 19.0	21.1, 19.2	11.6, 11.2	15.1, 14.7	6.9 × 10.3, 7.2 × 11.6	9.7, 10.3	3.5, 3.5
<i>chacoensis</i>							
ARGENTINA							
Río de Oro <sup>8</sup>	—	17.0	10.8	12.0	5.3 × —	8.2	2.7
BRAZIL							
Lagôa Santa <sup>10</sup>	—	—	9.5	11.0	4.9 <sup>5</sup> × 7.3	8.0	—

<sup>6</sup> Type of *gnambiquarae* Miranda Ribeiro, from original description. — <sup>7</sup> Juvenal, cootype of *gnambiquarae*, skull only (B. M. 21.6.3.1.) figured infra pls. 10, 12—15. — <sup>8</sup> Measured on dry skin. — <sup>9</sup> Type of *chacoensis* Gyldenstolpe; external measurements from dry skin. —

<sup>10</sup> Type of *fronto* Winge from original description and figure of skull.



Genus KUNSLA (nov.)<sup>5</sup>

*Scapteromys*, Gyldenstolpe (part, not WATERHOUSE), 1932, Kungl. Sv. Vet. Akad. Handl., 11, (3):98 – part species, *tomentosus* Lichtenstein, *chacoensis* Gyldenstolpe, *gnambiquarae* Miranda Ribeiro. ELLERMAN, 1943, Families and genera of living rodents, 2:425–426 – part, *tomentosus*, *chacoensis*, *gnambiquarae*. CABRERA, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia", 4, (2):474 – part, classification.

Type species. – *Mus tomentosus* Lichtenstein.

Included species. – *Kunsia tomentosus* Lichtenstein, *fronto* Winge.

## Distribution

(Map, figure 1)

Mixed savanna-forest regions of the highlands or planaltos of Brazil from Minas Gerais west through Mato Grosso and possibly Rondonia, into the uplands of Beni, Bolivia, southward through the Río Paraguay–Uruguay–Paraná basin to northern Argentina; altitudinal range between sea level and 1000 meters above.

## Characters

External. – Size large to largest of living cricetines; external form adapted for fossorial and palustrine life; tail (fig. 2) short, fore and hind feet (figs. 4, 5) large, powerful and provided with extremely long claws with those of forefeet longer; pelage coarse, thick on upper parts, comparatively thin on underparts; upper parts and sides of head and body dark brown coarsely mixed with grayish, buffy, orange or tawny; underparts more or less defined from sides, dark hairs with grayish to buffy subterminal bands; tail thick proximally, tapering strongly distally, uniformly dark brown or blackish, the hairs hispid and fairly long proximally, becoming gradually shorter or vestigial terminally, three to six hairs to each scale, scales large and exposed throughout, keel hairs and pencil absent; length of tail from less than one-half to two thirds of head and body combined; ears (fig. 3) small, rounded, moderately well haired inside and out; forefoot stout, vestigial pollex with thickened nail-like claw, digits II–V short, claws well curved with each longer than corresponding digit; plantar tubercles enlarged, digital bristles sparse and poorly developed; hind foot stout and broad, length, dry (with claw) between 16%–20% of head and body combined, claws stout, of middle digits moderately curved inferiorly and nearly as long as corresponding digits; interdigital webbing poorly developed between middle digits, absent on outer, digital bristles moderately developed, plantar pads enlarged with fifth postdigital pad present.

Cranial (pls. 6, 8–15). – Skull robust, the bones moderately thick to heavy with occipital, temporal and superior masseteric ridges well developed; rostrum heavy and comparatively short; nasals scalloped distally and moderately tapered proximally the ends forming an obtuse angle or truncate with a fine median spine extending slightly behind plane of fronto-maxillary suture; frontal sinuses not visibly inflated; zygomata heavy and well raised above alveolar level of molars; zygomatic plate nearly perpendicular, its anterior border closely approximated to preorbital foramen in front (pl. 3); rudimentary post-orbital process present; arc formed by fronto-parietal suture semicircular or greater; median parietal suture usually less than

<sup>5</sup> Named in honor of Dr. MERLE L. KUNS, of the Middle American Research Unit, National Institutes of Health, investigating hemorrhagic fever in Bolivia. Dr. KUNS was particularly concerned with rodent reservoirs of the disease and was responsible for the collection of mammals which included first known Bolivian representatives of the remarkable genus now bearing his name.

one-half as long as median frontal suture; hamular process of squamosal (temporal) short, broad, completely overlapping dorsal segment of temporal vacuity and much of ventral segment; supraoccipital usually concave dorso laterally not inflated medially and characterized by a broad sagittal crest; mastoidal capsule (periotic) not visibly inflated; mandibular ramus strong, broad and at least one-half as high as greatest length of mandible without incisor; capsular projection forming a prominent tubercular process midway between coronoid and condylar processes.

Dental (fig. 6; pls. 16, 18). — Incisors moderately heavy, color of upper and lower normally orange; occlusal surface of slightly worn molars plane (slightly terraced in molars of suckling young), general outline of worn  $m_1$ – $m_2$  E-shaped, of  $m_2$ – $m_3$  E- or S-shaped;  $m^2$  about as wide as long; lower first molar with 4 roots; mesoloph absent in available specimen of *Kunsia tomentosus* with unworn molars and vestigial but clearly defined in *K. fronto*; mesolophid absent; anterior median fold absent (vestigial in newly erupted first molars); first upper primary fold of  $m^2$ – $m^3$  reduced and isolated in worn molars, second upper primary fold of moderately worn molars with persistent though constricted marginal opening; first primary fold of  $m_1$ – $m_2$  with constricted opening to margin except in greatly worn molars, lower second primary isolated in moderately worn first and second molars, obsolete in third and erased in greatly worn molars; second secondary fold absent (isolated vestige present in newly erupted molars); paralophule and entolophulid if present, poorly developed and coalesced with mesostyle or mesostylid respectively.

### Comparisons

Characters distinguishing *Kunsia* from *Scapteromys* are included in the Key to the genera, the description of each genus and the discussion on adaptive radiation in scapteromyines (p. 87) and relationships (p. 96). Intraspecific comparisons are made in the species accounts.

### Key to the Species of *Kunsia*

Size large, head and body length more than 240 mm., tail more than half as long with six or more hairs per scale; rhinarium rimmed with whitish, underparts little or not at all defined from sides; alveolar length of molar row more than 9 mm., width of  $m^1$  more than 3 mm. . . . . *tomentosus* (p. 117)

Size smaller, head and body length less than 240, tail half as long or less with three hairs per scale; rhinarium bordered with brown; underparts moderately well defined from sides; alveolar length of molar row less than 9 mm., width of  $m^1$  less than 3 mm. . . . . *fronto* (p. 113)

### *Kunsia fronto* Winge

(Synonymies under the subspecies headings)

#### Distribution (Map, Figures 1, 7)

Known only from the planalto do Brazil in Minas Gerais as fossil and from Río de Oro, Chaco, Argentina as living. The species probably is still extant in the Río Paraná basin from the Brazilian highlands to the Argentine Chaco.

## Characters

Size as in *Rattus rattus* but tail proportionately short; form adapted for fossorial and aquatic life; pelage coarse but not harsh, tawny mixed with dark brown on upper parts, the cover hairs slaty basally, annulated buffy subterminally, the tips blackish; ears (fig. 3), muzzle and upper parts of fore and hind feet (figs. 4, 5) brown with a light buffy mixture; underparts whitish or pale gray lightly washed with buffy or yellowish, the dark basal portions of the hairs showing through; tail (fig. 2) about one half or less combined head and body length, hairs hispid, brown above, paler beneath and shorter distally than proximally, three hairs to each scale, keel hairs and pencil absent, scales moderately enlarged and showing through; hind foot stout and moderately elongate; skull moderately heavy, temporal (occipital?) and superior masseteric ridges present (pls. 6, 10, 12, 14, 15); proximal ends of nasals extending behind plane of fronto-maxillary suture to form an obtuse triangle; other cranial characters and dentition as described for the genus.

## Comparisons

*Kunsia fronto* is intermediate in size between its congener *K. tomentosus* and *Scapteromys tumidus* but, presumably, without overlap in most measurements with adults

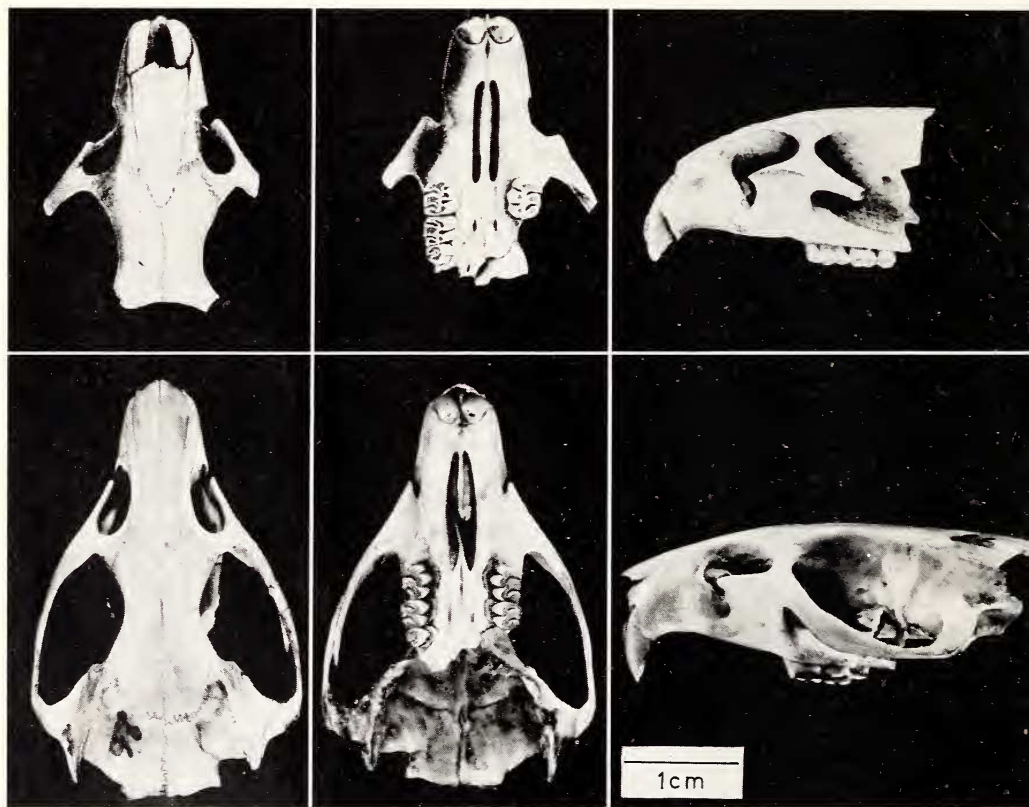


Plate 6. Skulls of *Kunsia fronto*: Upper row, *Kunsia fronto fronto* Winge, type, reproduced from the original figure. Lower row, *Kunsia fronto chacoensis* Gyldenstolpe, type.

of either species. In color pattern, *chacoensis* resembles *tumidus* but the character of the pelage is as in *tomentosus*; hind foot proportions, pelage length and scutellation of tail and size of molars are also intermediate but structurally most of these characters are more nearly as in *tomentosus*. In general, *fronto* appears to be a model from which the larger more stoutly built and more highly specialized *tomentosus* can be derived.

### Relationships

WINGE's *fronto* is a small, primitive species of *Kunsia* and not a large, highly specialized species of *Scapteromys*. The characters of *fronto* which appear to be intermediate between those of the larger *Kunsia tomentosus* and the smaller *Scapteromys tumidus* are related to the first phyletically and only metrically to the second. In those characters where allometric growth alone results in seemingly important differences in size and proportions between large and small individuals of the same or related species, the intermediate sized *fronto* is not intermediate in grade of development or juvenal-like in appearance as compared with *tumidus* and *tomentosus* respectively. It is, rather, surprisingly similar to the larger *tomentosus*. In fact, *fronto*, judged by two fragmented skulls, has attained nearly or quite the same grade of evolution in the flare of the zygomatic arches, specialization of the zygomatic plate, broadening and shortening of the nasals behind, enlargement of the vertical portion of the mandibular ramus, thickening of incisors, specialization of molars and all other characters mentioned in the description of the genus (pls. 6, 10, 12, 14, 15).

*Kunsia fronto* stands near, perhaps directly on the line leading to *tomentosus* (pls. 1-4). There are, however, traits suggesting a divergence on the part of *fronto* but present material is too deficient and defective for their evaluation. The extremely short tail of *fronto* for example, appears to represent a significant departure from the *tomentosus* line and an even greater one from the *tumidus* line. However, external characters of *Kunsia fronto* are known from a single skin with tail tip missing and little can be said of their evolution that is not speculative.

### Taxonomy

Cranial and dental characters of scapteromyines are so distinctive that absence of significant differences between the type skulls of *chacoensis* and *fronto* is regarded as *prima facie* evidence of conspecificity. GYLDENSTOLPE (1932:2) had already noted the very close resemblance between the types but dismissed the likelihood of their identity because "their respective type localities are situated far from each other". Taxonomic value attached to mileage is dubious and in this case may be unworthy of consideration. Subspecific distinction based on size and color, however, is a possibility. Until external characters of Brazilian *fronto* are known, tentative recognition of the Argentine *chacoensis* as a subspecies, is recommended.

### Remarks

Only two specimens of *fronto* are known. One is the type of *chacoensis* represented by a poorly prepared skin with right hind leg missing, skull (pls. 14-16) with posterior half and ventral whole of braincase and left  $m^3$  missing and mandibular angles incomplete. The second is the fragmented type skull of *fronto* (pl. 6). Oddly, the remnants of both type skulls are of the same parts so that little of what is lacking in the one can be reconstructed from the other.

Nothing is known of the habits of *fronto* and not much can be surmised of its



habitat. In general, *Kunsia fronto* appears to be less fossorial and more palustrine or aquatic than *K. tomentosus*.

*Kunsia fronto fronto* Winge

*Scapteromys fronto* Winge, 1888, E. Mus. Lundii, 1, (3):44, pl. 3, fig. 3 (skull).

Types. — Anterior portion of skull (figured) and mandible of another individual, Copenhagen Zoological Museum; collected in 1839 by P. W. LUND.

Type locality. — Pleistocene cave deposits (Lapa da Escrivania no. 5), Lagôa Santa, Rio das Velhas, Minas Gerais, Brazil.

Distribution (map. fig. 1) — Known only from type locality, the Pleistocene deposits in Lagôa Santa, Brazil, but range possibly extends or formerly extended north in Minas Gerais through the Rio das Velhas basin, west and south into the Paraná basin at least in Minas Gerais and São Paulo.

Characters. — Those of the species. The original description, freely translated from Danish, follows:

"Only a few fossil fragments in Lapa da Escrivania nr. 5.

"Known only from the anterior part of a skull [pl. 6].

"It is closely related to *Scapteromys principalis* from which it differs by the following characters.

"It is smaller.

"Outer wall of infraorbital foramen [zygomatic plate] lower, upper wall [infraorbital bridge] more oblique downward and outward. Nasal sinuses more inflated behind, the frontal more arched and without constriction; interorbital borders smoothly rounded; posterior ends of nasals pointed and produced farther behind [the frontomaxillary sutures] but this may be individually variable.

"Measurements of the figured skull, an adult:

"Upper molar row . . . . .	8 [mm]
"Upper incisors, combined width . . . . .	3 <sup>1</sup> / <sub>2</sub>
"Upper m <sup>1</sup> to incisor [diastema] . . . . .	11
"Palatal width between second molars . . . . .	4
"Length of incisive foramina . . . . .	9 <sup>1</sup> / <sub>2</sub>
"Height of zygomatic plate . . . . .	7 <sup>1</sup> / <sub>3</sub>
"Interorbital width . . . . .	7

"Measurements of a mandible, adult, surely of the same species:

"Lower molar row . . . . .	9
"Mandibular length . . . . .	25 <sup>2</sup> / <sub>3</sub> "

Specimens examined. — None.

*Scapteromys fronto chacoensis* Gyldenstolpe

*Scapteromys chacoensis* Gyldenstolpe, 1932, Ark. Zool. Stockholm, 24B, no. 1:1. GYLDENSTOLPE, 1932, Kungl. Sv. Vet. Akad. Handl., 11, (3):99, pl. 12, fig. 1 (skull of type), pl. 18, fig. 5 (molars of type) — Argentina: Chaco Austral (Río de Oro). YEPES, 1938, Rev. Centro Estud., 2:161 (separate) — Argentina: Chaco Austral (Río de Oro); FORMOSA, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia", 4:475 — probably a subspecies of *S. gnambiquarae* [!].

Type. — Male, skin and skull, Royal Natural History Museum, Stockholm, no. 26, collected September, 1896, by A. Ros.

Type locality. — Río de Oro, Chaco, Argentina.



**Distribution** (maps, figs. 1,7) — Known only from type locality but range probably extends northwest through the Paraguay-Paraná basin into Paraguay and Mato Grosso, Brazil, east into Misiones, Argentina and the southeastern states of Brazil.

**Characters.** — Those of the species.

**Measurements.** — See Table 5, page 110.

**Specimens examined.** — 1. Argentina. Chaco: Río de Oro, 1 (NRS, type of *Scapteromys chacoensis*).

### **Kunsia tomentosus** Lichtenstein

(Synonymies under the subspecies headings)

#### **Distribution** (Map, Figure 1)

The highlands of Brazil from Minas Gerais, Mato Grosso and neighboring parts of Rondonia and uplands of Beni, Bolivia, to undetermined limits southward in the Río Paraná basin; unknown in Paraguay, Uruguay and Argentina; altitudinal range between 200 and 1000 meters above sea level.

#### **Characters**

Size largest and heaviest of living cricetines; form specialized for fossorial life; pelage harsh, upper parts and sides of body dark brown, ticked with grayish or buff, the dark basal portions of the hairs appearing as a dark lining; ears (fig. 3), muzzle and upper surface of fore and hind feet brown mixed with gray, rhinarium with a conspicuous border of white hairs; underparts not defined from sides of body, hairs dark gray basally, buffy to gray or whitish terminally; tail (fig. 2) from over one-half to two-thirds length of head and body combined, hair dark brown to black, hispid, shorter on distal portion of tail than proximal and reduced or vestigial on under surface of terminal one half, scales extremely large with six bristles each, sometimes only three bristles on distal portion of tail; fore and hind feet (figs. 4, 5) extremely broad and stout; skull (pls. 8–10, 12, 14, 15) heavy with strong occipital and temporal ridges, proximal ends of nasals truncate with a fine median spine extending slightly behind plane of frontomaxillary suture; other cranial characters and dentition as described for the genus.

#### **Comparisons**

*Kunsia tomentosus* is the largest living cricetine. It may be matched in linear head and body dimensions by some extremely large water rats of the species *Nectomys squamipes* Brants, some marsh rats, species *Holochilus magnus* Herschkovitz, and large wood rats, particularly the species *Neotoma magister* Baird. None, however, compare with *Kunsia tomentosus* in sheer massiveness of head and bulk of body. Only members of the recently extinct West Indian oryzomyine genus *Megalomys*, with skull lengths ranging from 50–73 millimeters, equal and exceed *tomentosus* in all dimensions.

The pocket gopher-like adaptations for fossorial life in cricetines attain the highest degree of specialization in the present species. The claws of the forefeet of *tomentosus* are extremely long, sharp and recurved (fig. 4) and quite as well developed for digging as those of North American pocket gophers (Geomyidae) and their South American ecological equivalents, the tuco tucos of the caviomorph genus *Ctenomys*. The digits and carpus of *tomentosus* are correspondingly stout and powerful while the hind feet

including claws (fig. 5) are nearly as well adapted and even more specialized for digging than those of pocket gophers and tuco tucos. There is no evidence that *Ctenomys* and *Kunsia tomentosus* are truly sympatric but there are records of both from the *planalto* of Mato Grosso and other areas where *Kunsia* might be found.

The shortened and thinly haired tail (fig. 2) is another character shared by *tomentosus* with most fossorial rodents. The tail of *Kunsia fronto* may be even shorter but is not so thinly haired as to be nearly bare on the distal half of the underside as in *tomentosus*. In contrast, the caudal hairs of *Scapteromys* have elongated to form a keel and



Plate 7. *Kunsia tomentosus* Lichtenstein, type reproduced from the original colored plate (somewhat less than  $\frac{1}{4}$  natural size).

well defined pencil. The double number ( $2 \times 3$ ) of hairs per caudal scale in *tomentosus* is deceptive. Actually, the scale, whether by enlargement or by fusion of two, is double-sized and forms around twice the usual number of hairs. The large scale with 6 stiff hairs probably braces the tail in burrowing or in resisting predators. The worn and clipped hairs of the nearly bare undersurface of the tail point to such use.

The external ears of *tomentosus* (fig. 3) have also become smaller as an adaptation to fossorial life. Although still well developed they are significantly smaller (12%) in proportion to combined head and body length than those of the subfossorial *Scapteromys* (14%) and considerably smaller than those of such non-fossorial cricetines as phyllotines (over 20%).

The coarse nearly hispid iron gray fur of *Kunsia tomentosus* recalls that of the grison (*Galictis*) or the dark phase coat of the jaguarundi (*Herpailurus*). The coloration is uncommon in cricetines but the fur can be closely matched in color and texture with some dark races of *Sigmodon hispidus*, notably the Florida cotton rat, *S. hispidus littoralis*. The fur of *S. fronto* is also *Sigmodon*-like but differs from that of *tomentosus* by being thicker and more tawny, the underparts grayish and clearly but not sharply defined from sides. The coat of *tomentosus* differs markedly from the thick soft pelage of most species of fossorial rodents.

The heavy skull of *Kunsia tomentosus*, as in fossorial rodents in general, is designed to provide more surface for larger masticatory and cervical muscles. The fully developed occipital crests together with the forward inclination of that bone, accommodate muscles for powerful movements of the entire head in support of the movements of the lower jaws in biting and tearing through hard soils and tough roots. The same cranial adaptations are present in *K. fronto* but are much less developed. The skull of *Scapteromys* is comparatively delicate and its evolution appears to be directed toward reduction of the cranial musculature and degeneration of the incisors, mandibles and zygomata (pls. 1-4).

## Habits and Habitat

*Kunsia tomentosus* is a burrowing animal of the Brazilian campos and the tree-savanna plains of Mojos, Bolivia. It may live almost entirely underground during most of the dry season and mostly above ground during periods of heavy rains or inundations. Perhaps because of the animal's large size and powerful body it has never been captured in ordinary snap traps. The few known preserved skins are of individuals seized by hand or by dogs. MIRANDA RIBEIRO (1914:38, 39) mentions that the skin of one of his four specimens of *S. gnambiquarae* was damaged by dogs. The same authority adds that the Parecis Indians call the animal *colori* while the Nhambiquaras know it as *arantacú* and regard the flesh as a culinary delicacy. The *colori*, notes MIRANDA RIBEIRO, lives in burrows and makes a nest of dry grass. It feeds on the roots of grasses exposed in tunneling.

The two available specimens of *Kunsia tomentosus* were collected by the Middle American Research Unit of the National Institutes of Health in connection with its search for reservoirs and vectors of Bolivian hemorrhagic fever. The first specimen was brought to Dr. MERLE KUNS on 1 October 1963, by a native worker who retrieved it from a dog which had killed it in the vicinity of San Joaquín. The second specimen was live-trapped 5 December, 1963, by RAUL CANDÍA, the foreman of Dr. KUNS' team of Bolivian field assistants. According to Dr. KUNS (in litt.) CANDÍA captured the large rat in an open savanna some 50 yards from a forested "island" known as Isla Redonda de Caravana, about 15 kilometers north of San Joaquín. This remarkable and very rare rat was the only animal taken in 50 live traps set 3 nights in the area. Dr. KUNS concludes with the painful note that RAUL CANDÍA was bitten on the finger by a *Calomys callosus* while livetrapping, marking and releasing mice in San Joaquín. The open wound was contaminated with urine from the same animal. Shortly thereafter, CANDÍA was stricken by hemorrhagic fever and died Friday, March 13.

## Remarks

Despite its large size and utilization as food by the local Indians, *Kunsia tomentosus* is one of the rarest of rodents in museum collections. Known preserved specimens are the type skin and shattered skull in the Berlin Museum, the fragmented type skull of *principalis* Lund together with a remnant of a juvenal skull and some mandibles in the Copenhagen museum, four cotypes of *gnambiquarae* Miranda Ribeiro of which a skin with skull and a skeleton only are in the National Museum of Rio de Janeiro, and a skin with skull and a juvenal in spirits with skull separate in the British Museum (Natural History) and, finally, the two skins and skulls recently collected in Bolivia by the Middle America Research Unit, National Institutes of Health.

*Kunsia tomentosus tomentosus* Lichtenstein (pl. 7)

*Mus tomentosus* Lichtenstein, 1830, Darstellung neuer Säugeth., 7, (15): pl. 33, fig. 1 (animal) and text.

[*Hesperomys* (*Scapteromys*)] *tomentosus*, Peters, 1860, Abh. Akad. Wiss. Berlin, p. 147, pl. 2, fig. 2 (teeth) – classification; cranial and dental characters of type in Berlin Museum. PETERS, 1860, Monatsb. Akad. Wiss. Berlin, 1860:135 – classification.

*H[esperomys] (Scapteromys) tomentosus*, Thomas, 1884, Proc. Zool. Soc. London, 1884: 449 – classification.

[*Scapteromys*] *tomentosus*, Trouessart, 1897, Cat. Mamm., p. 534 – classification.

*S[capteromys] tomentosus*, Thomas, 1920, Ann. Mag. Nat. Hist., (9), 5:477 and footnote – comparisons; "Prof. MATSCHIE informs me that SELLOW's collection were made near Maldonado, where *S. tumidus* was obtained by DARWIN."

*Scapteromys gnambiquarae* Miranda Ribeiro, 1914, Comm. Linhas Telegr. Mato Grosso, Anexo 5, Mamm., p. 37, pl. 20 (skin), pls. 21, 22 (skeleton) – Brazil: Mato Grosso (type loca-



lity, Campos Novos, restricted by MOOJEN, 1952, Os roedores do Brasil, p. 80); Riacho Lanbary; Ultimo Acampamento, Chapada); cotypes, 1 skin and skull, 1 skeleton only in Museu Nacional, Rio de Janeiro and 2 skins and skulls in British Museum (Natural History), collectors, HOENE and MIRANDA RIBEIRO (the skull only); local name, *colori* (Parecis), *arantacú* (Nhambiquara). CABRERA, 1961, Rev. Mus. Argentino Cienc. Nat. "Bernardino Rivadavia", 4:475 — may be a synonym of *S. principalis* Lund of the Brazilian Pleistocene.

Type. — Adult female, skin formerly mounted and fragmented skull removed from mounted skin, Zoological Museum, Humboldt University, Berlin, no. 1699; collected 1827, by Herr SELLOW.

Type locality. — "Von Herrn SELLOW im Jahre 1827 in den waldigen Gegenden am Uruguay entdeckt", i. e., wooded parts along the Río Uruguay. The type may have been taken somewhere along the river's course in southeastern Brazil (Rio Grande do Sul or Santa Catarina) in wooded parts of northwestern Uruguay or in Misiones, Entre Ríos, or Corrientes, Argentina. According to THOMAS (1920), Ann. Mag. Nat. Hist., (9), 5:477, footnote) "Prof. MATSCHIE informs . . . that SELLOW's collections were made near Maldonado, where *S. tumidus* was obtained by DARWIN." This is most unlikely. The specimen almost certainly does not occur anywhere in Uruguay except possibly in the northwestern corner. In any case, it is a matter of record that SELLOW collected in southeastern Brazil and along the Rio Uruguay (cf. PELZELN, 1883:13). In addition, he secured specimens from other collectors, local dealers and from the museum in Montevideo, Uruguay. There is no good reason for believing that the type of *Mus tomentosus* was collected in any place other than the one given by LICHTENSTEIN and I hereby restrict it to the Rio Uruguay in southeastern Brazil. Further restriction awaits discovery of a Brazilian specimen with precise locality data.

Distribution (Map, fig. 1). — The Bolivian uplands of northern Beni, the planalto of Mato Grosso and the Río Paraná basin between southern Brazil and northern Uruguay; altitudinal range between 200 and 1000 meters above sea level; limits of range unknown but may be those of the species.

Characters. — Those of the species.

Measurements. — See Table 5, page 110.

Taxonomy. — The original specimen of *Mus tomentosus* Lichtenstein was mounted with skull in and exhibited in the Berlin Museum. Three decades later PETERS (1861:147) removed the skull from the hardened skin for the purpose of determining the true relationship of the species. The skull (pl. 12) was shattered in the removal operation but PETERS recognized the overall resemblance of LICHTENSTEIN's rat to *Scapteromys tumidus* Waterhouse and he assigned the former to the genus of the latter. The present color of upper parts of head and body of the type is brownish ticked with buffy, sides paler and underparts buffy with the dark basal gray of the hairs showing through, tail uniformly brown, ears and upper surface of fore and hind feet pale brown, the digits paler than the metapodials. The overall cinnamon brown coloration may seem to be natural but the original description and color plate of the type reproduced here (pl. 7) are of a "black-gray" animal. Obviously, the skin has become bleached through exposure to daylight and the chemical action of preservatives used in its preparation.

The original description of *Mus tomentosus* follows.

„Artkennzeichen: Um vieles größer und stärker als die gemeine Ratte, mit kurzen Hinterfüßen, wenig verlängertem Schwanz und breiten runden Ohren. Die Farbe glänzend schwarz-grau, Mitte der Bauchseite matt aschgrau. Behaarung dicht und weich.

Maße: Ganze Länge von der Schnauze bis zur Schwanzwurzel . . . 11 Zoll — Lin.  
 Länge des Schwanzes . . . . . 6 Zoll — Lin.  
 Länge des Kopfes bis zum Nacken . . . . . 3 Zoll — Lin.  
 Länge der Ohren 1 Zoll; Breite derselben . . . . . 1 Zoll 3 Lin.  
 Länge des Hinterfußes vom Hacken bis zur Krallenspitze . . . 2 Zoll — Lin.



Jedes einzelne Haar ist auf dem Grunde tief schwarzgrau, dann glänzend schwarzbraun und an der äußersten Spitze weiß. Nur die Spitze der Nase und beide Lippen sind weiß, von der Oberlippe zieht sich zu beiden Seiten ein kaum merklicher weißer Strich über dem Mundwinkel hin, die Spitzen der Zehen sind weißlich, die daran sitzenden Nägel schmutzig gelbgrau. Der Schwanz ist in seiner ersten Hälfte mit ganz schwarzbraunen glänzenden Haaren bewachsen, in der letzten mit breiten Schuppenringen bedeckt, zwischen welchen an der Oberseite ziemlich lange vereinzelt braune Borsten hervorwachsen, indessen die Unterseite ganz kahl ist. Die Ohren sind an dem Rande der inneren Wölbung mehr als an der Außenseite mit Haar von der Leibesfarbe bewachsen. Bartborsten werden kaum sichtbar. Die Vorderzähne sind nach außen gelb.“

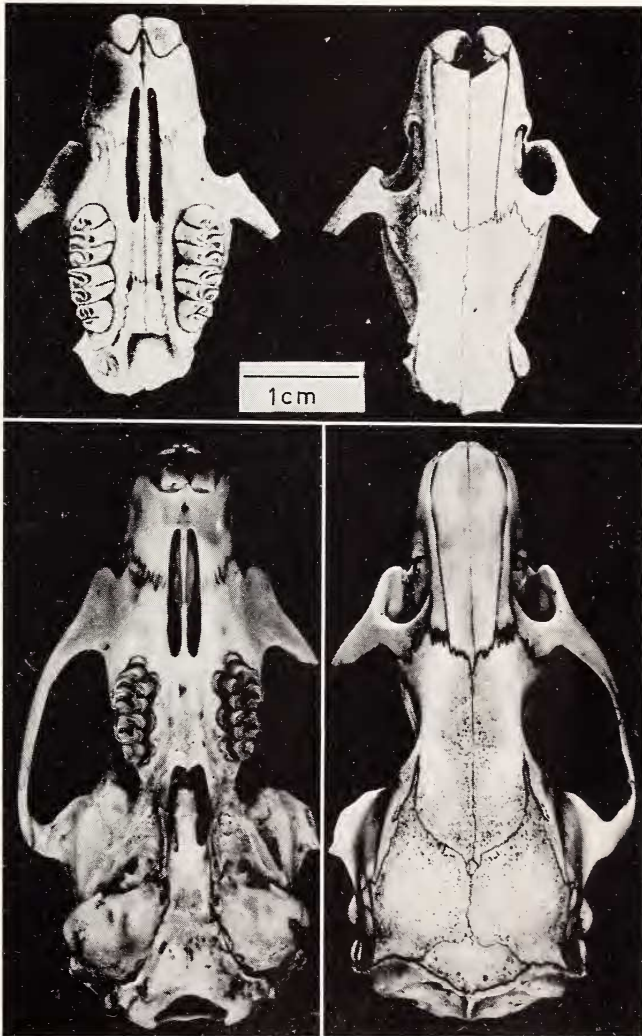


Plate 8. Skulls of *Kunsia tomentosus*: Upper row, *Kunsia tomentosus principalis* Lund, type, reproduced from the figure by WINGE (1888, pl. 3, fig. 2). Lower row, *Kunsia tomentosus tomentosus* Lichtenstein (San Joaquín, Bolivia).

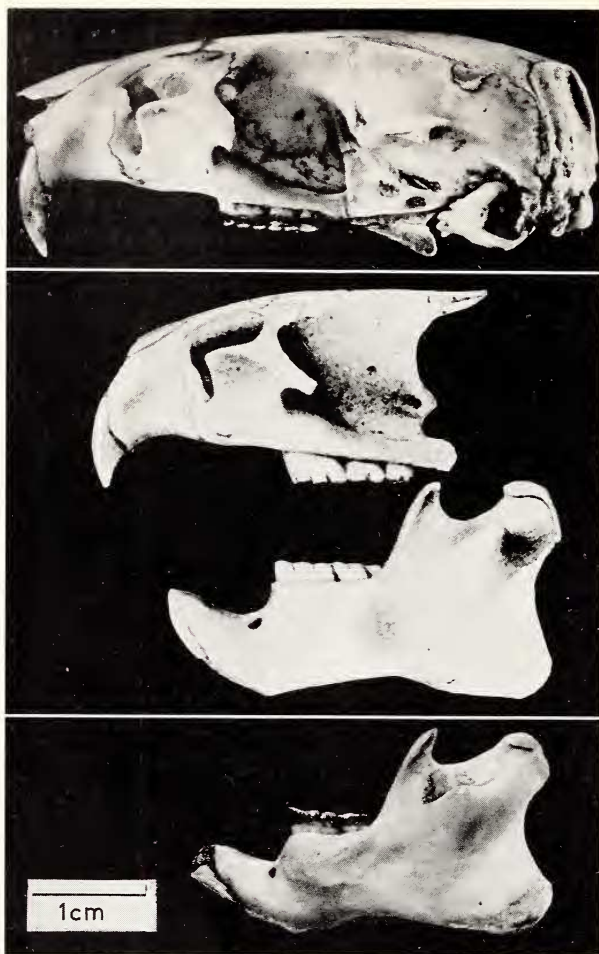


Plate 9. Skulls of *Kunsia tomentosus*: Upper and lower figures, *Kunsia tomentosus tomentosus* Lichtenstein (San Joaquín, Bolivia); middle figures, *Kunsia tomentosus principalis* Lund, type, reproduced from the figure by WINGE (1888, pl. 3, fig. 2).

Specimens examined. — 4. BRAZIL. MATO GROSSO: near Chapada, 1 (BM, cotype of *Scapteromys gnambiquarae*); BOLIVIA: BENI: San Joaquín, 2 (uncatalogued); COUNTRY UNKNOWN. "Waldregion Gegenden am Uruguay", 1 (BZM, type of *Mus tomentosus*).

*Scapteromys tomentosus principalis* Lund (pls. 8, 9)

*Mus principalis* Lund, 1839, Ann. Sci. Nat., Paris, (2), 12:208 — nomen nudum; BRAZIL: MINAS GERAIS (Rio das Velhas). LUND, 1840, Ann. Sci. Nat., Paris, (2), 13:312 — nomen nudum.

*Mus principalis*, Lund, 1841, Afh. K. Danske Vid. Selsk. Nat. Math., 8:276, 280, 294.

[*Hesperomys (Megalomys)*] *principalis*, Trouessart, 1880, Bull. Soc. Etud. Scient. Angers, 10, (1) 134 — classification.

*Scapteromys principalis*, Winge, 1888, E Mus Lundii, 1, (3): 42, pl. 3, fig. 2 (skull) — BRAZIL: MINAS GERAIS (Lagôa Santa); characters.

*Scapteromys gnambiquarae* Miranda Ribeiro is based on four specimens, one a skeleton only, none designated holotype. The description is of the skeleton and one or more skins including that of a female from which the mammary formula was determined. MIRANDA RIBEIRO pointed to *principalis* Lund as the most nearly related species and said it differed by the position of the optic foramen on the frontal suture outside the orbit, posterior profile of skull less elevated [!], nasals and intermaxillaries longer, m<sup>1</sup> with anterior lobe expanded anteriorly. The fragmented skull of *principalis* lacks the posterior half and one wonders if the posterior profile and other distinctive characters may not belong to *gnambiquarae* itself. The original description and figures of the skull of a juvenal cotype of *gnambiquarae* at hand (pls. 10, 14–16, 18), agree with the type of *tomentosus* and our specimens from Bolivia. There appears to be no basis for recognizing *gnambiquarae* even as a subspecies.

Types. — Anterior two thirds of an adult skull without mandible, one fragment of a juvenal skull and a number of mandibles only (19 listed by WINGE, 1888:43); lectotypes are skull of one individual and mandibles of another figured by WINGE (1888: pl. 3, fig. 2), Zoological Museum, Copenhagen, collected 1839 by PETER WILHELM LUND.

Type locality. — Pleistocene and Recent cave deposits (Lapa da Escrivania no. 5), Lagôa Santa, Rio das Velhas, Minas Gerais, Brazil.

Distribution (Map, fig. 1). — Known only from Pleistocene fossils and Recent owl pellets found in the caves of Lagôa Santa, Minas Gerais, eastern Brazil.

Characters. — Cranial and dental characters those of the species, external characters unknown.

Measurements. — See Table 5.

Taxonomy. — The original description of *principalis* is inadequate but WINGE's detailed account and finely executed drawing of the skull and teeth (pls. 8, 9) leave no doubt of their pertinence to specimens of *tomentosus* at hand. Even MIRANDA RIBEIRO recognized all but absolute identity between *principalis* and Mato Grosso representatives of the species he named *gnambiquarae*.

Remarks. — Although not recorded since 1839 there is no reason to believe that this retiring rodent has become extinct in Minas Gerais.

## II. A REVIEW OF THE MALE PHALLUS IN MURID CLASSIFICATION

### Introduction

A series of studies of the murid glans penis by HOOPER (1958, 1959, 1960, 1962), by HOOPER and HART (1962) and by HOOPER and MUSSER (1964a, 1964b) add considerable data to our knowledge of the interrelationships of many species, genera and supergeneric groups within the family Muridae. The findings of these authors support some concepts of generic and supergeneric relationships based on non-phallic characters and baculum alone and question and impugn others.

In 1959, HOOPER distinguished a group of North American cricetines characterized by a simple penis with single pronged baculum from other murids with complex penis and essentially three pronged baculum. He (p. 10) observed that "a classification based on anatomy of the phallus may not jibe with current classifications which are founded largely on cranial, especially dental, characters. It remains to be seen which of the two schemes most likely reflects the true relationships of muroid rodents."

In 1962, HOOPER and HART reviewed the classification of North American microtines on the basis of phallic characters. Their studies also extended to cranial, dental and external characters. The broadened base permitted them to observe that classifications of microtines derived from single characters whether external, cranial or dental are typological and wanting. Teeth alone, they (p. 63) emphasize "constitute no panacea in classification of microtines. Neither does the glans penis." This organ, they declare, "merely adds additional data to the total available for estimates of microtine interrelationships." Later, in a proposed arrangement of the species of the genus *Peromyscus*, HOOPER and MUSSER (1964b:10) affirm that although "the basis for [their] classification is primarily data derived from the glans and baculum . . . each grouping of species is definable on the basis of characters of study skin, skull [excluding dentition], male phallus and habitus." These qualifications constitute a repu-



diation of the earlier insinuation (above) that phallic and non-phallic characters are mutually exclusive with one reflecting true relationships, the other not.

It would appear that there is no need to belabor HOOPER and associates, whether HART or MUSSER, on the inadequacies and pitfalls of single character and typological taxonomy. This makes it all the more incomprehensible why HOOPER and MUSSER (1964a) revert to HOOPER's earlier (1959) posture and adopt phallic characters alone as the touchstone of murid classification in general and neotropical cricetines in particular.

### Methodology and Taxonomy

Use of male phallic characters in classification adds a very important dimension to mammalian taxonomy. The value of such characters in any given taxon, however, cannot be properly assessed from one or a few organs and without reference to the organism as a whole. The number of suitable glans penises of neotropical cricetines used by HOOPER and MUSSER (1964a) is inadequate for any assay at classification. The data they obtained, often from only one or two samples, are used nevertheless, without qualm or qualification for adducing relationships and revising currently recognized systematic positions of species, genera and supergeneric groups. Evidence from nonphallic characters pointing in other directions are unheeded or brushed aside. Even supporting evidence in these quarters are treated only slightly less cavalierly. Female genitalia, the complement of male genitalia and the other half of phallic evolution are disregarded. Geographic and historical data are completely excluded. In many instances individual, local and geographic variables in male phallic structures are deemed good taxonomic characters or suspected of being atypical, artificial or misidentified to taxon. Evidence of intraspecific and interspecific variation in male phallic characters presented by other authors (cf. HERSHKOVITZ, 1962: 58-68; also Pocock, 1925, with particular references to cercopithecids) are ignored. Clear evidence in their own material of parallel evolution or convergence in phallic characters is with one exception, passed over unrecognized or misinterpreted. The assumption that phallic differences represent taxonomic differences and that phallic similarities preclude taxonomic differences generally prevails throughout the work. The solitary relationship admitted between the phallus and other parts of the organism is the ratio of glans length to foot length. A ratio between two such morphologically and functionally separate and unrelated members, however, is misleading. This ratio may have served HOOPER (1958) as a happy guideline in some peromyscines. In murines and Neotropical cricetines (cf. HERSHKOVITZ, 1960:522, 1962:51) the hind foot assumes a great diversity of shapes and proportions in many different lines of evolution, while the penis varies independently<sup>6</sup>.

The taxonomic approach used by HOOPER and MUSSER is insistently and unremittingly phallic and typological. Indeed, so obsessed are the authors with the overriding importance of phallic characters that they speak of the species, genus or generic group where only the glans penis of one or a few individuals should be mentioned. This confusion of concepts has resulted in some conclusions that are premature or rash and others that are divisive and retrogressive. Had HOOPER and MUSSER concentrated their efforts on a reconstruction of the evolution of the organ they studied instead of

<sup>6</sup> The true relationship between morphologically distinct and topographically separated organs is through the organism as a whole. The ratio of glans penis length to combined head and body length and the ratio of hind foot length to combined head and body length are meaningful. On the other hand, the ratio of penis length to length of hind foot or of tail, snout, ear or any other appendage is an abstraction of no taxonomic or evolutionary significance.



attempting to construct phylogenies of organisms they did not study, they might have brought us nearer to a solution of some problems of muroid systematics.

## Material

HOOPER and MUSSER (1964a:5—6) examined 175 glandes of 43 neotropical species belonging to 16 genera. Included are 32 glandes from *Oryzomys caliginosus*, and 12 from *O. albigularis*, but the majority of the species are represented by 3 or less glandes (11 species by 1 glans penis each, 8 by 2, and 8 by 3). Table 1 on page 8 of the work cited shows the actual number of glandes suitable for effective descriptions, comparisons and phylogenetic interpretations. There are 121 such glandes representing 39 species and 16 genera. Thirty one species, or 82% of the total, are represented by 3 or less glandes (13 by 1 each, 10 by 2 and 8 by 3). More than half the total number of glandes (68) represent 12 nominal (but 8 or 9 valid) species of *Oryzomys*.

The glandes are described by HOOPER and MUSSER within the framework of generic groups as currently classified. My review and interpretation follow their arrangement but with the scapteromyines and oryzomyines placed at the end for convenience.

## Thomasomyine Group

Members of the thomasomyine group are sylvan and adapted for arboreal or scansorial life. Five genera and a large number of species are recognized. HOOPER and MUSSER (p. 19) examined the glandes of monotypic *Nyctomys*, monotypic *Otonyctomys*, *Rhipidomys* (1 species of a probable 6) and *Thomasomys* (3 species of a probable 30). Monotypic *Phaenomys* is not represented in their material<sup>7</sup>.

Morphological peculiarities in the glans penis of *Nyctomys sumichrasti* move HOOPER and MUSSER to divorce it from the thomasomyine group. *Thomasomys aureus* (1 defective glans) is not, according to HOOPER and MUSSER (p. 44), a thomasomyine. *Rhipidomys mastacalis*, judged by its glans alone, differs nearly as much as *Thomasomys aureus* does from *T. cinereus* and *T. laniger*, the only other species of *Thomasomys* known to HOOPER and MUSSER. The glandes of *Thomasomys cinereus* (1 glans) and *T. laniger* (5 glandes) also point in other directions. Their exterior configuration resembles, according to HOOPER and MUSSER (loc. cit.), "that in some oryzomyines (e. g. *O. palustris* and *O. concolor*), the narrow non-spinous crater collar is like that in *Oxymycterus* and some *Akodon*, spininess of crater and contents as in some *Akodon* and *Calomys*, characters of dorsal papilla and urethral flap approaching conditions in *Akodon* and shape of bone somewhat resembling that in *Sigmodon* and *Rheomys*." In effect, phallic characters indicate that *Thomasomys*, as known to HOOPER and MUSSER, is anything except *Thomasomys*. Exclusion, by inference, of all other genera from thomasomyines reduces the group to a chimera.

*Otonyctomys*, the glans of which was belatedly examined (footnote, p. 49) is described as "a well differentiated form which may be more closely related to *Nyctomys* and *Thomasomys aureus* than to other Neotropical forms examined. In the diagram of possible relationships (fig. 8b) it might fit as an independent offshoot between those two genera [sic]." The cited figure shows the offshoot position between *Nyctomys* and (genus?) "*T. aureus*", occupied by *Scapteromys*.

<sup>7</sup> The thomasomyine group is unrevised, its diagnostic characters loosely defined (cf. HERSHKOVITZ, 1962:21, 22, 55, 56). Thomasomyines include the most primitive of cricetines. They are forest dwelling, broad footed, long tailed, 6-mammate, brachydont-pentalophodont mice with wide-short palate and weakly projecting zygomatic plate. They compose one of the more coherent of the multigeneric groups of South American rodents. Some of the characters shared by the members of the group may be phenetic rather than phyletic but this has yet to be determined.

*Nyctomys* is of particular interest. It together with *Otonyctomys* are the only complex penis cricetine genera confined to North America. According to HOOPER and MUSSER (op. cit., p. 41) the "affinities of *N[yctomys] sumichrasti* are somewhat obscure. In some of its characters it appears to be annectant between the neotomyines-peromyscines and the clusters of South American forms. In shape of glans and nature of spinous investiture it recalls *Ochrotomys*, *Otodylomys* and *Tylomys*; the papilliform lateral mounds resemble similarly located papillae in *Tylomys*; the elevated meatus urinarius approaches the condition seen in *Scotinomys* and *Baiomys*; and the slender long bone with its distal cap of cartilage is not unlike the configuration of baculum seen in neotomyines and peromyscines. BURT (1960:63) saw resemblances in the bacula of *Neotoma* and *Nyctomys*.

"On the other hand, the vascular lobes, three bacular mounds, multilobed urethral flap and some other characters appear to relate *Nyctomys* to the mass of South American species. We tentatively view it as a highly [p. 42] differentiated outlier of that group though we cannot readily overlook its several similarities with neotomyines-peromyscines. Clearly, as judged from our samples, *Nyctomys* is unlike *Rhipidomys* with which it has been aligned (TATE, 1932a; HERSHKOVITZ, 1962); it does not belong closely with either *Rhipidomys* or *Thomasomys* as we know them."

Some peromyscines (*Peromyscus*, *Megadontomys*, *Ochrotomys*) had been once (cf. HERSHKOVITZ, 1944:20, footnote 7) included among the thomasomyines. The dichotomy between simple and complex penis types was not then suspected. It now appears that *Nyctomys*, judged by phallic and non-phallic characters, may indeed be a link connecting peromyscines and thomasomyines to a common Middle American ancestor (cf. HERSHKOVITZ, 1944:20). In New World cricetines, evolution of the complex to simple penis by reduction and elimination of the lateral bacular digits may be traced through thomasomyines from *Rhipidomys mastacalis*, *Thomasomys aureus*, *Nyctomys* and *Otonyctomys* to peromyscines.

Other peculiarities of the genital tract which seemingly connect *Nyctomys* morphologically with peromyscines, particularly *Neotoma*, have been discovered by ARATA (1964:14, 31) in the accessory reproductive glands. ARATA saw no preputial, vesicular or dorsal prostate glands in the single specimen examined of *Nyctomys sumichrasti* and the three he examined of *Neotoma floridana*. Ventral prostates also lacking in *Nyctomys* are, however, present in *Neotoma*. Other simple penis type cricetines with missing accessory glands are, according to ARATA, *Peromyscus gossypinus* and *Reithrodontomys humulus* without preputials, *Ochrotomys nuttalli* and *Onychomys leucogaster* without ampullaries, and *Onychomys leucogaster* and *Tylomys nudicaudus* without anterior prostates. The accessory glands absent in *Nyctomys* and some peromyscines are found in all the complex penis type species ARATA examined. These are *Oryzomys palustris*, *Oecomys tectus* (*concolor*), *Nectomys alfarí*, *Akodon* sp., *Phyllotis darwini*, *Sigmodon hispidus*. Unfortunately, ARATA studied only one species of each of 15 cricetine genera. Except for *Sigmodon hispidus* with 50 samples and *Oryzomys palustris* with 10, all but three of the remaining species in ARATA's material are represented by 1 or 2 specimens, the others by 3, 4 and 5, respectively. At this point, it can be said that simplification of the penis in *Nyctomys* and peromyscines frequently entails the loss of one or more accessory reproductive glands excluding the bulbo-urethral which is always present. Simplification and loss of parts are almost certainly independent processes in each group and, possibly, in each genus.

### Akodont Group

The akodont group has not been critically examined and the nominate genus is urgently in need of taxonomic revision. HOOPER and MUSSER studied the glands of 8 of 30 "species" of *Akodon* listed by CABRERA (1961:437–461)<sup>8</sup>. This genus, according to HOOPER and MUSSER (op. cit., p. 24) "is recognizable by a combination of characters none of which is unique. In size and proportions it overlaps oryzomyines and phyllotines and its other traits are separately approached or matched in species of *Calomys*, *Eligmodontia*, *Phyllotis* or *Zygodontomys*." Ignoring "size and proportions" as probably misleading characters, the "other traits" suggest that *Akodon* is phallically most like phyllotines, a conclusion in harmony with previous estimates based on non-phallic characters.

An example of intraspecific variation in phallic characters disturbs HOOPER and MUSSER. They (op. cit., p. 24) note that „two adult specimens of *A[kodon] arviculoides* at hand do not match in morphology, age or geography." The gross differences between the glands (not figured) of the two mice, one from Misiones, Argentina, the other from Rio de Janeiro, Brazil, create "doubt that these distinctions are related entirely to the age difference between the two examples." The two mice in question are preserved in the Chicago Natural History Museum. Dr. HOOPER removed and labelled their phalli, I identified the animals at his request and later double checked the determinations.

### *Notiomys*

The genus *Notiomys*, known to HOOPER and MUSSER (p. 27) by 3 glands of *N. valdivianus*, differs from all other cricetines examined but "fits near or with our phyllotine and akodont species." This agrees in the broadest sense with data derived from cranial, dental and external characters.

### Oxymycterine Group

The oxymycterine group (see infra p. 86) comprises 4 nominal genera and 10 or 12 nominal species. HOOPER and MUSSER describe 1 glands of Bolivian *Oxymycterus paramensis* (= *O. rutilans paramensis* Thomas) and 5 glands of Uruguayan and Argentine *O. rufus* (= *O. rutilans rutilans* Olfers). Phallic differences between the three populations, particularly the Uruguayan and Argentine representatives of the same race, indicate a greater range of variation than HOOPER and MUSSER allow between some genera and generic groups.

The genus *Oxymycterus*, actually the species *Oxymycterus rutilans* which is treated as a generic group by HOOPER and MUSSER (op. cit., p. 45), "fits near the thomatomyine or akodont cluster" on the basis of its phallic characters. This appraisal is ambiguous. Thomasomyines and akodonts are widely separated. A species near the first group is not related to the second. *Oxymycterus* is a highly specialized shrew-like derivative of akodont stock. Whatever resemblance it has to thomatomyines is due to a remote common cricetine heritage and/or the result of convergence.

<sup>8</sup> I have excluded from CABRERA's arrangement of *Akodon*, "species" of the subgenus *Abrothrix* (an oxymycterine with 4 "species"), *Akodon mimus* (an *Abrothrix*), *Akodon iberingi* (an *Oxymycterus*) and *Akodon tapirapoanus* (a *Zygodontomys*). This last is listed by CABRERA as a species of *Akodon* on p. 447 and as a subspecies of *Akodon arviculoides* on p. 439. The status of *A. arviculoides* is uncertain as is that of many other species currently referred to *Akodon* (s. 1.).

## Phyllotine Group

The recently revised phyllotine group (HERSHKOVITZ, 1962) comprises 21 species distributed in 8 genera. HOOPER and MUSSER examined 13 glands of 8 species representing 4 genera.

The samples of these 8 species indicate to HOOPER and MUSSER (1964a:30) that phyllotines are "a diverse assemblage, one more varied than the oryzomine group, for example. They are well characterized at the generic level but some of them are no more similar to each other than some are to nonphyllotines." My findings, based on non-phallic characters and bacula, reveal these 8 species as radiating limbs of a common trunk. Evidently, their divergence is reflected in phallic as well as a number of non-phallic characters. The forms studied by HOOPER and MUSSER are reviewed below.

*Phyllotis*, as the central genus of the group is of special interest. HOOPER and MUSSER studied 5 glands representing 3 species (of 10 recognized). The authors (pp. 33–36) characterize the glands of *P. darwini* (1 adult), *griseoflavus* (2) and *pictus* (3, "none of which is old or otherwise entirely satisfactory") as "well differentiated from one another", and revive (p. 30) for each species the erstwhile discarded subgeneric names, *Phyllotis*, *Graomys* and *Auliscomys*, respectively. They add (p. 33) that "OSGOOD (1947), PEARSON (1958) and CABRERA (1961), but not HERSHKOVITZ (1962), arrange the species in separate subgenera." Obviously the first three authors cited could not possibly have disagreed with the fourth. In chronological order, CABRERA (1961:484) avowedly followed PEARSON (1958:395) who "focused [his] efforts on the species and subspecies level" and "made no special study of the generic and subgeneric relationships of *Phyllotis*". For these taxons, PEARSON followed ELLERMAN (1941:451) more closely than he did OSGOOD (1947). My revision of *Phyllotis* and phyllotines is a refinement and extension of OSGOOD's. Treatment of *darwini*, *griseoflavus* and *pictus* as three sharply defined species of *Phyllotis* (s. s.) is neither strengthened nor weakened by addition of the phallic characters described by HOOPER and MUSSER. Their account

of the glans penis of *Phyllotis darwini* gives no notion of the range of variation within the species (cf. fig. 9) much less the genus. Phallic, particularly bacular, differences they note between *P. darwini* and *P. griseoflavus* appear to be individual variables judged by material at hand and published data (PEARSON, 1958:424, fig. 6; HERSHKOVITZ, 1962:58–68, figs. 6–8).

*Calomys* is comprised of 4 tightly knit species but only the phallus of *C. laucha* (3+3 unsuitable glands) and *C. callosus* (1 glands) were studied. These two are the more distantly related species of the genus. Their glands are characterized by HOOPER and MUSSER (p. 48) as "similar". Nevertheless, their detailed description

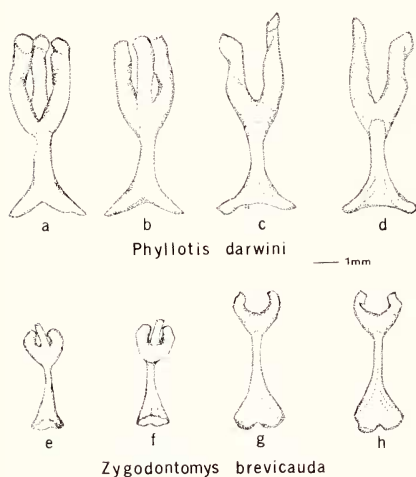


Fig. 9. Bacula of phyllotines, dorsal and ventral aspects, respectively, of a, b, *Phyllotis darwini* from Huancavelica, Peru (CNHM 75 455); c, d, individual variable (CNHM 75 453) from same series as preceding; e, f, *Zygodontomys brevicauda* from San Jerónimo, Antioquia, Colombia (CNHM 70 188); g, h, *Zygodontomys brevicauda* individual variable (CNHM 71 257) from Muzo, Boyacá, Colombia



indicates greater phallic differences between *callosus* and *laucha* than between *Phyllotis darwini* and *P. griseoflavus*.

*Zygodontomys*, according to HOOPER and MUSSER (p. 49) "belongs near *Oryzomys* or *Akodon* and not with *Calomys* and some *Phyllotis*". The authors appear to support their judgement with the reminder that *Zygodontomys* had at times been classified as an *Oryzomys* and at others as an *Akodon*. They might have added *Mus* and *Hesperomys* (= *Calomys*) as well. Species of *Zygodontomys* discovered during the 18th and 19th centuries were, like many other common mouse-like New World rodents, first referred to broadly conceived genera then shunted into successively more narrowly restricted genera until a special genus was erected for them. If phallic characters were everything HOOPER and MUSSER believe them to be, they would show that a taxon "near" *Oryzomys* is only remotely related to *Akodon* but a taxon near *Akodon* is also close to *Calomys* and *Phyllotis*. HOOPER and MUSSER's dendrogram (op. cit., p. 53) shows the position between *Oryzomys* and *Akodon* occupied by *Oxymycterus* while *Zygodontomys* is placed between *Sigmodon* (*Sigmomys*) and oryzomyines. Whatever its phallic characters, *Zygodontomys* cannot be more nearly related to *Oryzomys* than *Phyllotis* or *Akodon* on historic and geographic grounds alone.

The completely normal two and three digit bacula of *Zygodontomys* (fig. 9) illustrate individual variation within the species.

*Eligmodontia*, according to HOOPER and MUSSER (op. cit., p. 49), "perhaps also should be arranged nearer *Akodon*". In forming this opinion the authors (op. cit., pp. 33, 47) did too much with too little. They emphasize the small size of glans, baculum and hind foot of *Eligmodontia* and end by aligning the genus with those forms with which it agrees most nearly in overall size as well as size of its parts.

### Sigmodont Group

The sigmodont group consists of *Sigmodon* (*Sigmomys*), *Reithrodon*, *Holochilus* and *Neotomys*. In an earlier paper HOOPER (1962) published the description of 11 glands of *Sigmodon* (*alleni*, 3; *hispidus*, 5 adults, 1 subadult; *minimus*, 1 juvenile; *ochrognaethus*, 1 subadult), of *Sigmomys* (*alstoni*, 1 subadult) and of *Reithrodon* (*cuniculoides*, 1 adult). In their 1964 publication, HOOPER and MUSSER (p. 37) describe 5 glands of *Holochilus brasiliensis* (2 fluid preserved, 3 reconstituted from dry study skins). Glands of *Neotomys* were not available for examination.

Glands of sigmodonts examined appear to HOOPER and MUSSER (loc. cit.) as "a diverse lot, one which provides little support for the proposal that all species represented therein are closely related". Then shifting from glands to genera they conclude (op. cit., p. 50) that "*Holochilus* is an oryzomyine, and *Reithrodon* belongs near species of *Phyllotis*. *Sigmodon* and *Sigmomys* remain as sigmodonts."

That *Sigmodon* and *Sigmomys* are sigmodonts is redundant. They are congeneric (cf. HERSHKOVITZ, 1955:647<sup>9</sup>). Phallic differences between *Reithrodon* and *Holochilus brasiliensis* demonstrated by HOOPER (1962:7) and HOOPER and MUSSER (1964a:37) are not unexpected inasmuch as the taxons themselves differ widely. Nearness of sigmodonts, including *Reithrodon*, to phyllotines is also inferred from the phalli but this was already determined from non-phallic characters (cf. HERSHKOVITZ, 1955:644,

<sup>9</sup> My statement that *alstoni*, the single species of *Sigmomys*, was based on "individuals of South American representatives of *S[igmodon] hispidus* with grooved incisors" may have been too sweeping. Dr. CHARLES HANDLEY informs me that *alstoni* and *hispidus* are quite distinct where they are sympatric in parts of Venezuela.

1962:23, 25). Beyond, there is a combination of fundamental cranial, dental and external characters which unite *Sigmodon*, *Reithrodon*, *Neotomys* and *Holochilus* into a closely knit group. Superimposed upon this community of characters are one or more adaptive traits, phallic and non-phallic, peculiar to each radiating genus. Any classification based on these characters alone would indeed make sigmodonts or any other radiating group, „a diverse lot“.

Sigmodonts diverged from an old southern South American pastoral stock only remotely related to the northern, oryzomyine stock. *Sigmodon* radiated into the vole — or arvicanthine — like habitus. *Reithrodon* became the hare-like representative of the sigmodont group. *Neotomys* is a counterpart of microtines. *Holochilus* converged into the semi-aquatic equivalent of many other radiating murid clusters. *Holochilus* resembles large aquatic species of *Rattus* as well as the oryzomyine *Nectomys squamipes*, the smaller *Oryzomys palustris* and a number of other unrelated rodents not to mention insectivores. It is not strange, therefore, that with basic murid and cricetine similarities already built in, the phallus of *Holochilus* should also resemble that of *Oryzomys palustris*<sup>10</sup>, the nearest related of its ecological equivalents. Disregarding everything else, HOOPER and MUSSER interpret all phallic similarities as *ipso facto* proof of intimate kinship and transfer *Holochilus* to the oryzomyine group. The glans of *Sigmodon hispidus* with spine studded crater papillae is unique among neotropical cricetines, so far as known, but finds its analogue in the spine invested crater papillae of distantly related but ecologically similar species of voles (cf. HOOPER, 1962, fig. 1 and HOOPER and HART, 1962, figs. 8—10). In the light of basic non-phallic characters it would be just as absurd to classify *Sigmodon* as a microtine as it is to classify *Holochilus* as an oryzomyine (cf. HERSHKOVITZ, 1955:653—654).

### Ichthyomyine Group

The ichthyomyine group is made up of 5 unrevised genera (*Ichthyomys*, *Rheomys*, *Anotomys*, *Neusticomys*, *Daptomys*) each with one or two valid species. It is represented in HOOPER and MUSSER's material by three glandes of *Rheomys hartmanni*. According to these authorities (1964a:39), the organ of this species is well differentiated from that of others by a "unique assemblage of traits, but as appears usual among South American cricetines each single character is approached or matched in other species". In their dendrogram, HOOPER and MUSSER (op. cit., p. 53) arbitrarily assign *Rheomys* to a position between *Nyctomys* and *Sigmodon* near the base of the main branch of South American cricetines.

<sup>10</sup> An available glans penis of *Holochilus brasiliensis* from Uruguay (AMNH 206385) differs from that of *Oryzomys palustris* as described by HOOPER and MUSSER (1964a:12—13, fig. 1 ab) by comparatively smaller size, paratoid lobes weakly defined, dorsal papilla smooth except for an apical spine, subapical lobule of urethral flap present as described for *O. palustris* and *Holochilus brasiliensis* but it is proportionately much larger than illustrated for either and it is invested with spines. According to HOOPER and MUSSER, the urethral flap of all oryzomyines, and their specimens of *Holochilus brasiliensis* lack spines. In any case, a subapically lobulated flap is now known only in *Oryzomys palustris* and *Holochilus brasiliensis* among neotropical cricetines studied by HOOPER and MUSSER. A similarly lobulated urethral flap (or process) appears to be present in *Neotoma alleni* (HOOPER, 1960, pl. 8d) and in a number of microtines (HOOPER and HART, 1962). Evidently this structure with minor variations, has evolved independently in a number of lineages. Fundamentally, it does not differ from more symmetrically bilobed or trilobed urethral flaps, all derived from a simple flap.

## Scapteromyine Group

Material examined by HOOPER and MUSSER (1964a:29) consists of 3 glands from Argentine specimens labelled *Scapteromys aquaticus* and 2 imperfect glands from Uruguay determined as *Scapteromys tumidus*. Descriptions and comparisons of the glands of *Scapteromys tumidus* are given under a separate heading below. The genus, according to HOOPER and MUSSER (op. cit., p. 29), is "set well apart in morphology of glans from all other South American examples at our disposal". The authors continue (op. cit., p. 42) "in *Scapteromys* as in *Nyctomys* there are characters which resemble those of neotomyines. For example, the single bacular mound together with the peculiar shapes of urethral flap and baculum are reminiscent of features seen in the North American *Xenomys nelsoni* and *Neotoma allenii* (HOOPER, 1960). That there are resemblances with neotomyines is apparent, and the possibility that *Scapteromys* as well as *Nyctomys* is related to those forms deserves consideration. Certainly they are annectent forms in the sense that their characters bridge much of the morphological gap between the neotomyines and South American cricetines."

In the next paragraph HOOPER and MUSSER make an about face and point out that "the possibility that the resemblance with neotomyines were independently acquired is also apparent. The vascular system appears to be like that of the mass of South American species, not of neotomyines; the trilobed bacular mound and underlying cartilaginous mass appear to be strictly comparable to the three mounds and digits of the compound baculum, not to the simple baculum of neotomyines; and the multilobed dorsal papilla [!] and four-pronged urethral flap are features that are typical of microtines and other forms with a compound baculum. On the whole, our specimens of *S. aquaticus* and *S. tumidus* fit morphologically nearer those of other South American species than those of neotomyines or other forms studied to date. Total evidence from glans and baculum suggests that *aquaticus* and *tumidus* are strongly differentiated relatives of the other 41 sampled species."

The total evidence for proving the allocation of *Scapteromys* with South American rather than North American cricetines is overwhelming. Recourse to phallic characters alone for evidence is interesting but nevertheless redundant. The prior and perhaps stronger suggestion made by HOOPER and MUSSER that *Scapteromys*, judged by phallic characters, might stand nearer North American *Xenomys* and *Neotoma*, contravenes all other morphological evidence and violates present concepts of the origin, evolution and dispersal of South American cricetines with particular reference to *Scapteromys*. Even the intimation of a singularly close relationship between *Scapteromys* and Middle American *Nyctomys* and its implementation in their dendrogram (p. 53) finds absolutely no support in non-phallic characters and is completely refuted by phallic characters. Simplification of the glans in *Scapteromys* is accomplished by suppression of the medial digit, in *Nyctomys* and peromyscines by elimination of the lateral digits.

Of particular interest in their estimate of *Scapteromys* and *Nyctomys* is the rare, if not unique, concession made by HOOPER and MUSSER that phallic similarities may be independently acquired.

### *Scapteromys tumidus*

The following description of the glans penis is based on 3 fluid preserved specimens from Uruguay (fig. 10). Characters of the baculum are based on the 18 specimens (figs. 10–13) from Uruguay listed in Table 6.

Glans nearly twice as long as wide and laterally compressed (diameters x length in two specimens, 4.5 x 5.0 x 9.0 mm., 4.3 x 5.0 x 9.5 mm.; head and body length 167, 170 respectively); entire surface except crater walls densely set with spines; tapered

distal portion of glans furrowed longitudinally; skin of crater wall finely convoluted and distensible; bacular mound in one specimen simple and cirque-shaped with concavity dorsal (fig. 9e) triangular and triple peaked in two specimens with ventral peak slightly higher than laterals peaks (fig. 10a-b); finger-like dorsal papilla in depression of dorsal flank of bacular mound and studded with a large dorso-median spine; quadrilobate urethral flap slightly longer than wide, the inner lobes considerably narrower than outer and separated by a deep median cleft; lobes and tips and lateral borders of outer lobes of urethral flap spiny.

Baculum comparatively large, shovel-shaped and predominantly two-digitate, total length from three-fourths to nearly equal length of glans; base inflated often globose and defined from shaft by broadly sloping to sharply angled shoulders, dorsal surface convex, posterior border with or without a prominent median protrusion,

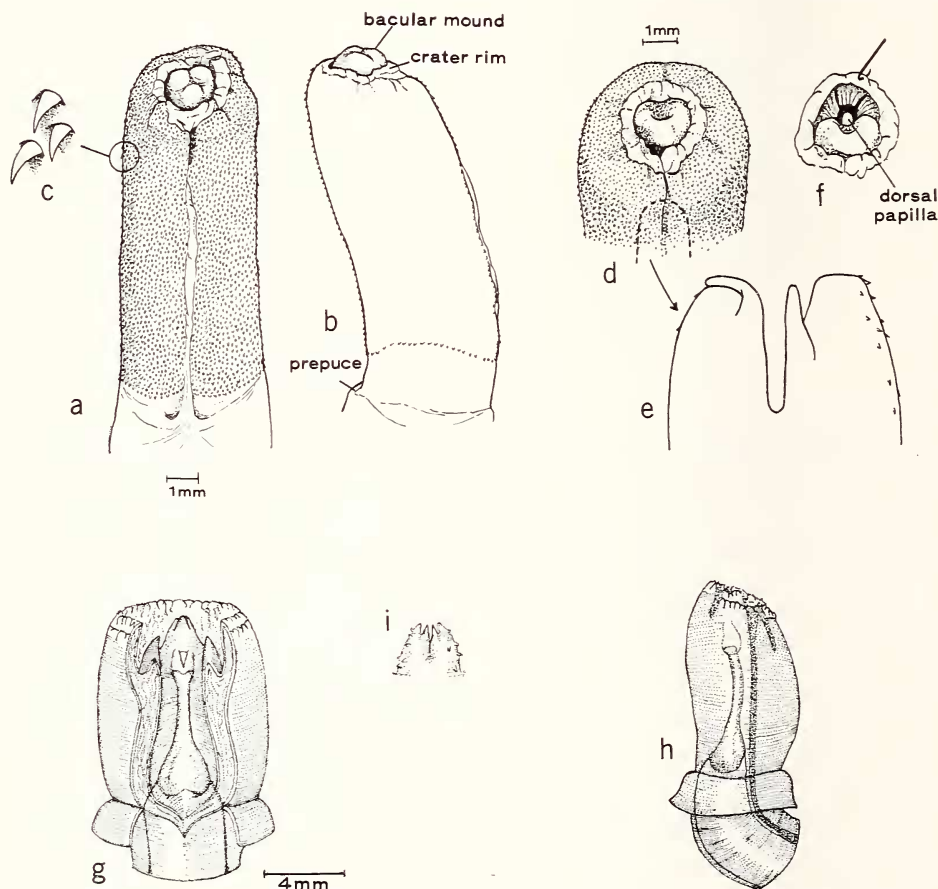


Fig. 10. Glans penis of *Scapteromys tumidus* (a to f from Uruguay); a. ventral surface (AMNH 206 226, Tropa Vieja, Canelones; head and body length, 170 mm.); b. same from right side; c. spines enlarged; d. glans penis, apical aspect (AMNH 206 211, Interbalneario, Km. 36, Canelones; head and body length, 167 mm.) showing bacular mounds in crater, broken lines show position and relative size of urethral flap; e. urethral flap from ventral surface, greatly enlarged, right side damaged and distorted; f. crater distended behind to expose dorsal papilla (diagrammatic!); g, h, i. (from Argentina) ventral and lateral aspects of glans to same scale, and ventral aspect of urethral flap enlarged (g-h redrawn from HOOPER und MUSSER, 1964a: figs. a-c).



rarely with a median concavity, ventral surface moderately concave to deeply and broadly hollowed; rounded shaft robust, dorsally bowed and frequently keeled ventrally, neck slightly constricted or, sometimes, with flattened lateral processes, head rounded and usually more or less bifurcate; distal bacular segment a relatively short, bud-shaped, four-peaked and dorsally concave matrix of diffuse cartilage; within matrix two densely cartilaginous digits each with a ventral prong or branch; third, or medial, digit greatly reduced, obsolete or, in most cases, absent; minute ossicles often present and usually scattered throughout cartilaginous envelope; bacular mound crescentic in horizontal outline with two lateral elevations corresponding to the lateral bacular digits or with a third, or ventral, elevation defined by thickly developed lateral digital prongs which approximate at mid ventral line (fig. 13).

**BODY CAVITY ACCESSORY REPRODUCTIVE GLANDS.** — The bulbourethral, ampullary, vesicular and prostates (dorsal, ventral and multilobate anterior) present; paired preputial glands large and expanded proximally in one adult examined, completely absent in two half grown individuals.

**REMARKS.** — Simplification of the bacular complex in *Scapteromys* has advanced by fusion of the lateral digits and elimination of the medial. In *Phyllotis* and *Zygodontomys* (figs. 9) the medial digit may be absent in some individuals but the lateral digits remain free and well developed.

The glans of *Scapteromys* figured by HOOPER and MUSSEY (1964: 30, fig. 7b, c) and reproduced here (fig. 10) is about the same in size and general form as the three specimens described above but differs in some details. The dorsal papilla is said to be "situated in [sic] a ridge of the dorsal flank of the bacular mound. Lobules adjacent to the finger (these spine tipped in some specimens) may also be vascularly protractile parts of the papilla; if so the structure is compound (multilobulate)." In our specimens the dorsal papilla is simple and rests in a recess of the bacular mound. The distal portion of the urethral flap of HOOPER and MUSSEY's specimen is shown

Table 6

*Scapteromys tumidus*: measurements in millimeters of bacula arranged in order of decreasing size of the animals sampled

AMNH No.	Locality	Total Length	Baculum Proximal Bone	Width	Head and Body	Greatest Length of Skull
206 244	Barra del Arroyo	7.8	6.7	2.5	197	40.4
206 208	36 km. E. Montevideo	7.8	6.8	3.2	194	—
206 270	3 km. E. Cardona	8.4	7.3	3.2	188	—
206 324	Río Tacuari	8.3	7.5	3.2	187	—
206 263	Río Santa Lucía	9.1	7.9	3.2	185	41.5
206 268	3 km. E. Cardona	8.4	7.3	3.2	184	—
206 283	3 km. E. Cardona	9.1	7.5	3.4	182	41.4
206 300	3 km. E. Cardona	7.3	6.1	2.9	181	41.2
206 319	Río Tacuari	8.0	7.1	3.1	180	40.0
206 316	Río Tacuari	7.7	6.8	3.2	180	39.8
206 322	Río Tacuari	7.3	6.2	2.8	170	39.7
206 273	3 km. E. Cardona	7.5	6.0	3.0	168	40.3
206 320	Río Tacuari	7.2	6.3	3.4	168	—
206 241	Estancia Las Marías	7.4	6.4	2.9	167	40.4
206 278	3 km. E. Cardona	6.9	6.1	2.5	167	—
206 246	Barra del Arroyo	6.5	6.0	1.4	167	—
206 330	Río Tacuari	8.0	6.2	3.0	162	40.9
206 274	3 km. E. Cardona	7.1	6.0	3.0	157	40.9
206 281 imm.	3 km. E. Cardona	5.7	4.8	1.6	149	—
206 217 imm.	36 km. E. Montevideo	5.9	4.7	1.8	146	36.6

(fig. 7b) divided into four nearly equal lobules. This contrasts with the small inner and much larger outer lobules of present specimens. Three samples examined by HOOPER and MUSSER are from Buenos Aires (possibly Punta Lara), Argentina and identified as *Scapteromys aquaticus*. The two specimens from Canelones, Uruguay, determined as *Scapteromys tumidus*, are said to be similar to *aquaticus* but "may differ in regard to dorsal papilla and shape of bone (a midventral keel and larger, laterally expanded head in the examples of *tumidus*." The difference "in regard to dorsal papilla is not indicated while and the differences in shape of baculum are individual variables. MASSOIA and FORNES (1964:283) find the penises and bacula of Uruguayan and Argentine swamp rats indistinguishable.

HOOPER and MUSSER (p. 30) regard the baculum of *Scapteromys* as "short". This may be an inadvertent error. The mean length of three specimens of *Scapteromys* is given (op. cit., p. 8) as 6.9 mm. This dimension is exceeded by the measurements of only 3 or 4 of the 39 tabulated forms. The means and extremes of 16 bacula of fully adult specimens at hand (Table 6) are 7.6 (6.9–9.1). Only *Thomasomys aureus* with glans length given by HOOPER and MUSSER (loc. cit.) as 12.6 mm., is longer. It seems from these figures that two of HOOPER and MUSSER's three specimens may be immature. The sample they figure (op. cit., p. 4, fig. 7c) and reproduced here (fig. 10) is certainly an immature. If by "short" HOOPER and MUSSER mean the ratio of glans

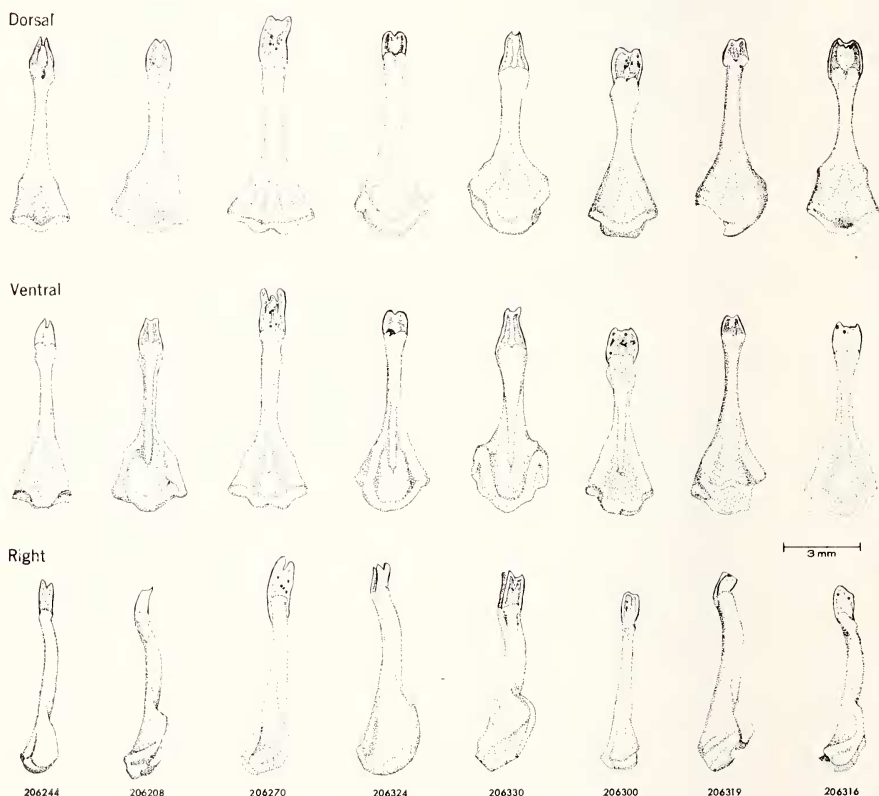


Fig. 11. Bacula of *Scapteromys tumidus*, dorsal (upper row), ventral (middle row) and right lateral (lower row) (continued in fig. 12 opposite); samples arranged in order of length of head and body, or skull. See pages 132, 133 for details. Samples cleared in KOH and stained with alizarin; all specimens in the American Museum of Natural History.

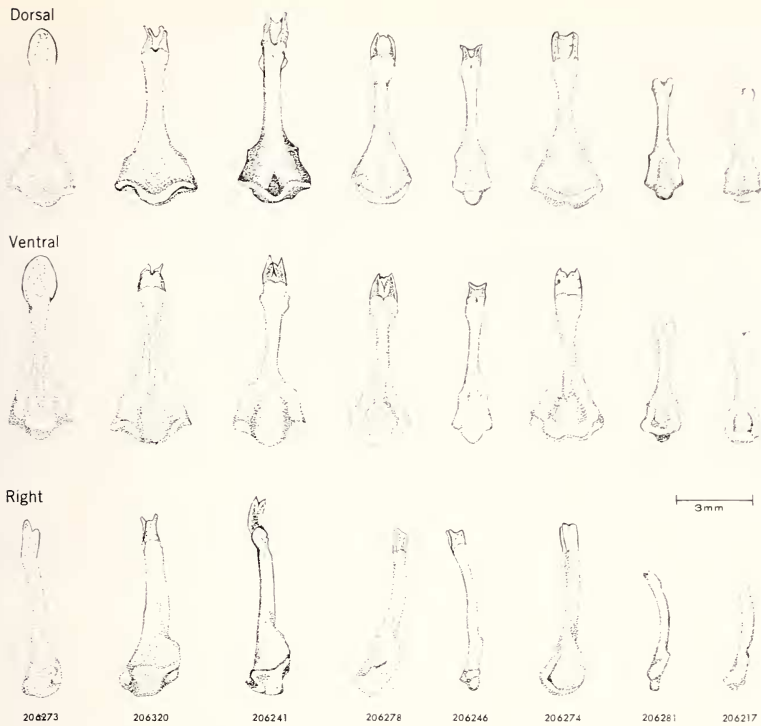


Fig. 12. Bacula of *Scapteromys tumidus* continued from fig. 11.

length to hind foot length (op. cit., p. 10) they inadvertently distort the true relationships. In *Scapteromys* it is not the penis that is short but the hind foot that is long (cf. op. cit., table 8) and there is no intrinsic taxonomic value in the proportion of foot length to penis length.

### Oryzomyine Group

Oryzomyines studied by HOOPER and MUSSEY are represented by a greater number of glans penises from more species than any other group. The sampled species belong to 6 of the approximately 13 currently recognized oryzomyine genera and subgenera. Their phallic characters are described as fairly homogenous but "weakly characterized" (HOOPER and MUSSEY, 1964a:12). My studies of non-phallic characters of thousands of oryzomyines representing all known species convince me that oryzomyines constitute one of the most sharply defined multigeneric groups of murids. The assemblage is a classic example of high diversification with low suppression or distortion of stem characters (cf. HERSHKOVITZ, 1944:12-13; 1960:514).

*Neacomys* (*guianae* 4 glandes + 1 defective; *spinosis*, 2 defective) is sharply defined from all cricetines by its spiny pelage. Otherwise, it is distinctly oryzomyine and most nearly like *Oligoryzomys* in cranial, dental and external characters. Phallic characters as described by HOOPER and MUSSEY (op. cit., p. 17) fall in line with this estimate.

*Nectomys* is represented by 2 glandes of the referred species *N. (Sigmodontomys) alfari*. Its phallus is described (op. cit., p. 19) as resembling that of "*Oryzomys*

*caliginosus* and, especially, *O. alfaroi* . . . [The species] is unique among these and all other oryzomyines examined, however, in the nature of the spiny investiture of the glans." Judged by non-phallic characters, relationship between *N. alfari* and other species of the "*alfaroi* subgroup" is remote. The crucial comparison yet to be made is with the glans penis of type species *Nectomys squamipes*. Pending this and an overall revision of the oryzomyine group, the systematic position of *Sigmodontomys*, whether as subgenus of *Nectomys* or *Oryzomys*, remains unsettled (cf. HERSHKOVITZ, 1948:54, footnote 1).

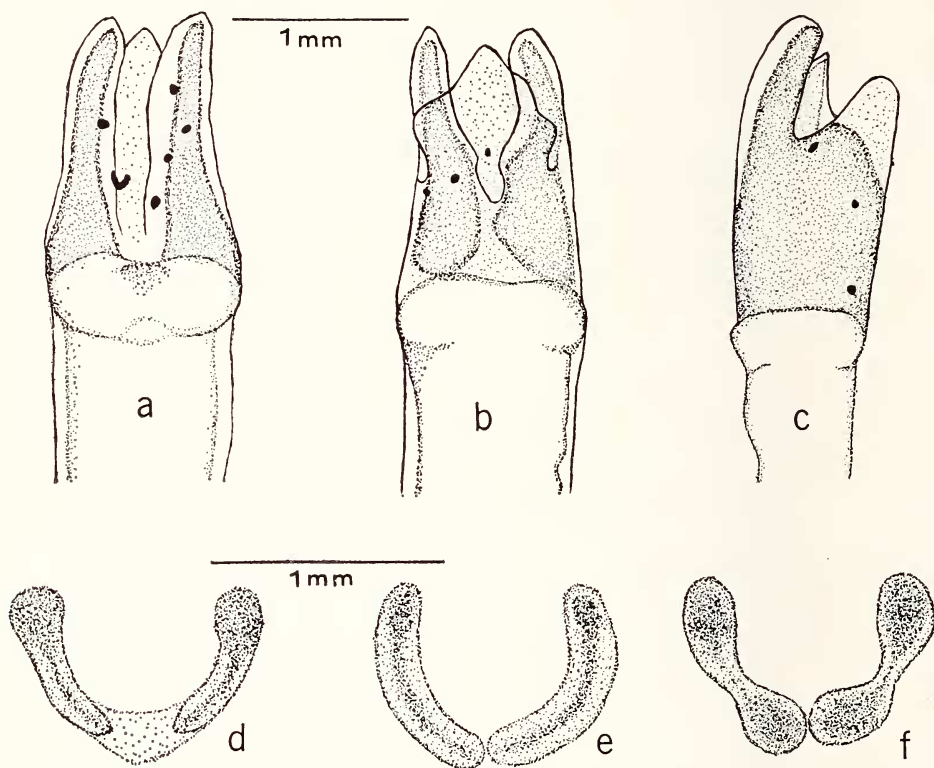


Fig. 13. Baculum of *Scapteromys tumidus* (Uruguay); distal digital portion; a-c. dorsal, ventral and right aspects of AMNH 206 270; d. apical aspect of same, concavity dorsal; e. AMNH 206 208; f. AMNH 206 241. Stippling corresponds to density of cartilage, ossicles shown in black; specimens cleared in KOH and stained with alizarin. For additional specimen data see page 133.

### Oryzomys

Using glans morphology as the basis, HOOPER and MUSSER (1964a:12) arrange their samples of *Oryzomys* by listing them in two divisions, the "*albigularis* subgroup" and the "*alfaroi* subgroup." For purposes of elucidation and convenience of reference and discussion, I list the members of each "subgroup" systematically. The species name is followed by the number of glandes studied plus (+) the number of defective or otherwise unsuitable glandes also taken into account by HOOPER and MUSSER. I add the approximate geographic range for the full species. Locality data for each specimen examined is provided by HOOPER and MUSSER (op. cit., pp. 5-6).



*"albigularis subgroup"**Oryzomys* (s. g.)

*palustris* (3 + 2): Southeastern U. S. (*palustris* complex) and lowlands of México and Middle America to northern Panamá (*cousi* complex).

*albigularis* <sup>11</sup> (11 + 1): Highlands of Costa Rica and bordering parts of Panamá (*devius*), western Panamá (*pirrensis*) and subtropical and temperate zone forests of Colombia, Venezuela, Ecuador, Peru and northern Bolivia.

*devius* (2): A race of *albigularis*. See above.

*capito* (9): Tropical forests of western Costa Rica, Panamá (*talamancae*) and South America.

*Oecomys* (s. g.)

*concolor* (6 + 1): Tropical and subtropical forests of Costa Rica, Panamá, Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Trinidad and Guianas.

*Oligoryzomys* (s. g.)

*nigripes* (1 + 1): Tropical to temperate zone forests and bordering savannas of Middle America (*fulvescens*) and South America (*nigripes* complex).

*fulvescens* (2 listed on p. 5, op. cit., 9 on p. 8): A race or species of the *nigripes* complex.

*flavescens* (3): A race of *nigripes*.

*longicaudatus* (4): A race of *nigripes*.

*"alfaroi subgroup"**Oryzomys* (s. g.)

*alfaroi* (3 + 2): Tropical to subtropical forests of Middle and South America.

*melanotis* (0 + 1): Lowlands of México.

*Melanomys* (s. g.)

*caliginosus* (16 + 16): Tropical to subtropical forests of Central America, Colombia and Ecuador.

The above arrangement shows that insofar as recognized species are concerned male phallic characters support the union of *devius* with *albigularis* ("closely similar") and of *flavescens*, *fulvescens* and *longicaudatus* with *nigripes* ("phallically similar if not identical"). Non-phallic characters hardly separate *Oryzomys alfaroi* from *O. melanotis* and HOOPER and MUSSER's findings agree. *Oryzomys palustris*, as represented by samples from Florida, Georgia and Texas, is morphologically, geographically and historically well separated from all other species of *Oryzomys*. HOOPER and MUSSER (op. cit., p. 45) conclude that this species stands "slightly apart from . . . [*albigularis* and allies] and other oryzomyines [and] we view it as our sole representative of a minor subgroup of oryzomyines." Thus far, phallic characters harmonize with non-phallic characters and what is known or inferred of the evolution and dispersal of the species in question.

As for the remaining species, it appears that for purposes of taxonomy little reliance can be placed on their phallic characters or HOOPER and MUSSER's interpretation of them. According to these authorities (op. cit., p. 45), "the [phallic] data do not support the subgeneric separation of *concolor* and *capito*." This may be true but subgeneric separation of *concolor* is premised on comparisons with *Oryzomys*

<sup>11</sup> For the specific synonyms of *albigularis* see HERSHKOVITZ (1944:72 and footnote). CABRERA (1961:380—383) recognizes most of them as nominal subspecies. Additional representatives of *albigularis* are *devius* Goldman, *villosus* J. A. Allen and *caracolus* Thomas. This last was inadvertently included by me (1960:544, footnote) among the specific synonyms of *Oryzomys laticeps* now *O. capito*. CABRERA (op. cit., p. 387) who read parts of the manuscript of my 1960 paper, followed suit and disposed of *caracolus* in the synonymy of *Oryzomys capito velutinus*. Pending comparisons with *O. albigularis meridensis* Thomas, the name of the northern Venezuelan form should stand as *Oryzomys albigularis caracolus* Thomas.

*palustris*, type of the genus *Oryzomys*. HOOPER and MUSSER have already indicated that phallically *O. palustris* stands apart from other oryzomyines. Elsewhere (HERSHKOVITZ, 1960) I have distinguished *Oecomys* as a subgenus on the basis of non-phallic characters. The same brief applies to subgenus *Oligoryzomys* which is taxonomically the most embroiled group of oryzomyines. *Oryzomys (Melanomys) caliginosus*, a member of the "*alfaroi* subgroup" of Hooper and Musser, shares many characters with other oryzomyines and its glans penis may resemble that of *alfaroi* more nearly than any others. Otherwise, *O. caliginosus* is one of the most distinctive species of the genus. *Nectomys (Sigmodontomys) alfaroi*, also included by HOOPER and MUSSER (op. cit., pp. 16, 46) in the *alfaroi* group, is no less differentiated than *O. caliginosus*, albeit in other characters.

Separation of *alfaroi* in one subgroup from *capito* in another highlights the inconsistencies between a classification based on a portion of a single organ, and one based on information from many sources particularly a knowledge of variation within and between populations. *O. capito* (or *talamancae*) and *O. alfaroi* can be distinguished by size and subtle cranial and dental characters where they are sympatric in Central America. In western Colombia and Ecuador the differences between *capito* and the smaller *alfaroi* become suspiciously narrow until in northern Peru *alfaroi* (now called *nitidus*) equals *capito* in all dimensions. Other differences remain tenuous or become insignificant. In the upper Amazonian region of tropical Ecuador and Peru, external, cranial and dental characters of the two evenly proportioned species persist in some populations, are recombined in others and in still others are randomly distributed without polarization toward one or the other phenotype. The same interplay of variabilities reappears in northeastern Brazil where the *alfaroi* type is known as *oniscus*. In southeastern Brazil the shifting roles of *capito* and *alfaroi* are enacted under the names *laticeps* and *intermedius*. Another nominal species, *Oryzomys lamia*, known from southern Brazil and Misiones, Argentina, enters as a third protagonist in this evolutionary interplay.

The *capito-alfaroi* patterns of variation and dispersal indicate that divergence began in South America, perhaps in the upper Amazonian valley. Invasion of Middle America by a population of either the "*alfaroi*" or "*capito*" chain provided conditions for speciation in isolation. Subsequent invasion of Middle America by representatives of the other chain completed a circular overlap with the ends of both chains most highly differentiated and completely isolated reproductively. This isolation may have had its beginnings in phallic variation and selection among individuals of the ancestral population.

*Holochilus brasiliensis*, according to HOOPER and MUSSER is also an oryzomyine, perhaps an *Oryzomys* of the "*albigularis* subgroup". These authors (op. cit., p. 45) conclude that the "striking and apparently fundamental resemblance [in phallic characters] of *Holochilus* and *Oryzomys* suggests that the position of *Holochilus* be reexamined with the thoughts in mind that it may be a well differentiated oryzomyine rather than a sigmodont". The presumption that the quintessence of mureoid taxonomy resides in a single character or a small part of a small organ should also be reexamined with the thought in mind that the name *Holochilus brasiliensis* may represent a multitude of very real and variable organisms with a long history in time and space rather than one or a few glans penises preserved in a vial. For my discussion of the status of *Holochilus brasiliensis*, see page 129, above.

### Penis Types in Murid Taxonomy

Studies of the male phallus by HOOPER and associates led to the recognition of two basic phallic types within the Muridae. These are the complex and simple. The

complex penis, they show, contains a baculum with typically three terminal digits and paired sac-like sinuses of the spongy tissue of the glans. This type obtains in murines, gerbillines, Old World cricetines, microtines, South American cricetines and probably others including otomyines and dendromurines. The simple penis they distinguished by the absence of lateral bacular digits and sacculations in the spongy vascular layer of the glans. This type characterizes a North American group of twelve genera arranged by HOOPER and MUSSER (1964a:54) in two intimately related tribes. These are the peromyscines with *Peromyscus*, *Reithrodontomys*, *Onychomys*, *Baiomys*, *Scotinomys*, *Ochrotomys* and *Neotodon* and the neotomyines with *Nelsonia*, *Ototylomys*, *Tylomys*, *Neotoma* and *Xenomys*<sup>12</sup>.

Simple and complex phallic types are not restricted to murids and neither type, so far as it has been described, distinguishes any murid taxon from all others. Peromyscines (including neotomyines), with simple penises, may be the one murid assemblage best defined by phallic characters. Nevertheless, HOOPER and MUSSER demonstrate simple or intermediate phallic types among Old World "cricetines" (*Mysopalax*, *Mystromys*), Neotropical "cricetines" (*Nyctomys*, *Scapteromys*), "microtines" (*Discrostonyx*, some species of *Microtus*, *Ellobius*, cf. HOOPER and HART, 1962) and nesomyines (*Macrotarsomys*). They allude (op. cit., p. 53) to a simple type penis among murines but found none in their samples (op. cit., p. 51). With the simple penis originating independently in all assemblages of murids (and Rodentia in general) it is not unreasonable to question whether the "neotomyines-peromyscines" of HOOPER and MUSSER represent a monophyletic group or an unnatural aggregation of two or more phallically convergent generic groups. ARATA (1964:27, fig. 9) using accessory reproductive glands as criteria arranges 7 of the 12 Holarctic cricetines with simple phalli into 4 groups which cut across the "peromyscines-neotomyines" of HOOPER and MUSSER.

Among murids with predominantly complex phalli, the Murinae, according to HOOPER and MUSSER (op. cit., p. 52), are most sharply defined. They list "15 murines of 12 genera or subgenera" (p. 50) as having been examined but describe none. Characters given for the collective are not impressive while the phallus of one genus, *Lophuromys*, is said to be aberrant. The phalli of hundreds of murine species yet to be studied will undoubtedly include many more "aberrations".

The Gerbillinae, conclude HOOPER and MUSSER (op. cit., p. 52), "belong together in regard to structure of phallus. Although distinctive, they resemble microtines and Old World cricetines." No supporting evidence is offered and no more information is given except for the statement that 4 samples of 3 genera were examined.

Seven Old World cricetines are said to have been studied. Their phalli are not described but the organs of *Myospalax* and *Mystromys* are said to be simple. HOOPER and MUSSER (op. cit., p. 54) suggest that these two genera may not be true cricetines.

The Microtinae are "characterized by ventral shield, crater rim papillae, and other features of glans and baculum [HOOPER and MUSSER, p. 52]." Elsewhere (HOOPER and HART, 1962:8, 54; HOOPER, 1962:4) it is said that crater rim papillae and a ventral shield are not constant microtine features.

A relatively small number of South American cricetines are described in detail (see above). Their phallic characters, according to HOOPER and MUSSER (op. cit., p. 54), "tie them to each of the preceding assemblages", i. e., murines, gerbillines,

<sup>12</sup> These twelve genera were first distinguished as simple penis types and arranged by HOOPER (1960) in four groups. In the same paper and in another published the previous year, HOOPER defined the complex and simple phallic types but alluded (1959:9) to "several basic patterns" of phalli in cricetines alone. The present critique is of the comprehensive and culminating HOOPER and MUSSER work wherein these authors temper earlier judgments.

microtines and Old World cricetines. The total evidence and particularly the characters of *Nyctomys* indicate rather that South American cricetines are much more nearly related to peromyscines.

The taxonomic value of male phallic characters in defining the Muridae as understood by HOOPER and MUSSER has not yet been properly assessed. Nevertheless, unity of the erstwhile unnaturally separated Cricetidae and Muridae of current classifications (cf. SIMPSON, 1945:83, 205; WOOD, 1955:176) is supported by phallic data although conclusively proven by other evidence most notably of the skull and teeth.

Present knowledge of phallic characters is also inadequate for defining the primary divisions of the family Muridae. No one phallic type is peculiar to any murid subfamily or coordinate assemblage. Rejection in the 18th century typological manner of phallically "non-typical" species does not enhance the taxonomic value of phallic characters for the remaining members of that group. Indeed, phallic characters of "non-typical" forms probably prove that differences between complex and simple types may be tenuous if not intergrading.

The value of phallic characters as adjuncts for defining certain genera and for distinguishing many species, providing limits of variation are known, is not questioned. HOOPER and associates have proven beyond doubt that wherever possible, appreciation of phallic characters must be a standard procedure in muroid taxonomy.

### Interrelationships of Murid Subgroups

The possible relationship of Old World cricetines, South American cricetines, microtines, gerbillines, murines and "peromyscines-neotomyines", based solely on characters of the glans penis are exhibited by HOOPER and MUSSER in the form of a dendrogram (1964a:53, fig. 8a).

If a time dimension is implied by the curving direction taken by the main stem and branches of the dendrogram then the arrangement of the subfamilial hierarchies clashes with much that is known of the evolution, dispersal and morphology of murids. For all their diversity, South American cricetines, living and fossil, include the most primitively structured murids. They are not most recently evolved as indicated in the dendrogram. On the other hand, living hamsters are highly evolved and far removed from near the base of the murid line where they are placed by HOOPER and MUSSER.

The simple penis "peromyscines-neotomyines" are shown forming a dichotomy with the complex penis cricetines of South America and like them ranked equally with the recognized subfamilies of Muridae. Why HOOPER and MUSSER fail to formalize analogous dichotomies of Old World assemblages where both phallic types also occur is not clear. However, there is no need for ambiguity here. HOOPER and MUSSER (op. cit., p. 52) argue convincingly that the "plain pene seen in some microtines, murines, South American cricetines and Old World cricetines are secondarily simple, derived from a complex-penis ancestral stock that gave rise to this mass of muroids. Similarly the glands of peromyscines and neotomyines then should also be considered as results of secondary reduction and loss of parts." In the absence of non-phallic evidence to the contrary it seems that each simple penis species or species group is best classified with the likely subfamily or tribe of its origin. Peromyscines (including neotomyines) are phallically specialized offshoots of the ancestral South American<sup>13</sup> cricetine stock. Peromyscines may have originated near the

<sup>13</sup> South American is used here in a generic and not a geographic sense. The ancestral South American cricetine stock was certainly North American, possibly Middle American.



base of the thomatomyine line (cf. HERSHKOVITZ, 1962:20) which includes *Nyctomys*. Phallically, they are farther removed from the bulk of South American cricetines than either *Nyctomys* or scapteromyines. Otherwise peromyscines and South American cricetines are essentially of a kind and familial and subfamilial distinction between them (cf. HOOPER, 1959:10; 1960:20) is not indicated. However, should a community of trenchant phallic and non-phallic characters be demonstrated for all peromyscines the propriety of tribal separation from Neotropical cricetines with complex phalli would be difficult to assail.

HOOPER and MUSSER (fig. 8b) also use a dendrogram for showing the inter-relationship between genera of Neotropical cricetines. Their arrangement, based on phallic characters only, makes a shambles of previous classifications founded on non-phallic characters. Their methods and data are critically reviewed in preceding sections.

### Phallic Evolution: The Lock and Key Hypothesis

The penis is designed for delivery of sperm in the female genital tract in a manner that insures fertilization of the egg. The penis is adapted to the size, shape, location and topography of the vagina and cervix, to the position and gravitational orientation of both male and female in coitus and to the normal habitat of the species during the breeding cycle or season. The mammalian penis also serves for marking the territory and for social and sexual display. These manifestations, however, are not universal and have not been studied in the rodents with which we are particularly concerned.

The elaborate glans penises of murids include devices which presumably inhibit premature withdrawal of the penis and reduce loss of semen deposited in the female genital tract. Theoretically, backwardly directed spines of the penial shaft deter withdrawal by the female. Climactic or second stage ballooning of the glans before and during orgasm likewise inhibits withdrawal by the male. The baculum facilitates maximum penetration and provides for firm fixation of the glans during and after the act. The waxy copulatory plug secreted through the urinary meatus prevents drain of semen from the vagina. Bleeding of the female genital tract from injuries caused by male phallic spines possibly facilitates movement of spermatozoa into the uterus and subsequent clotting may seal them in. The roles of urethral flaps, dorsal papilla and other specializations of the glans are not precisely known. They may be erectile, sensory or both while the urethral flaps may also control the ejaculation. All parts of the male phallus, however, may not be functionally oriented toward successful reproduction. Some organs may exert negative effects in particular cases and some mutations may contribute to sexual frustration and incompatibility.

The most important process in the evolution of the murid glans penis is reduction of the baculum from a complex three digit organ to a simple or single digit organ. Corresponding modifications usually take place in the bacular mounds. At the same time some accessory organs become reduced or lost, others enlarged and more complex and still others may appear as new. Simplification of the baculum, whether incipient or advanced, originates independently in all major groups of living murids. The process is continuous, irreversible and probably responds to selective pressures exerted by the female genital tract.

Simplification may proceed by reduction and elimination of the lateral digits as seems to have occurred in peromyscines, some murines (BITTERA, 1918:414) microtines (HOOPER and HART, 1962:23) and *Nyctomys* (HOOPER and MUSSER, 1964:22), by fusion of all digits as observed in *Scapteromys* (infra, p. 133, figs. 10–13) and by reduction and elimination of the middle digit resulting in a two-pronged baculum as noted in some *Scapteromys* and in individuals of *Phyllotis darwini* and *Zygo-*

*dontomys brevicauda* (infra, p. 128, fig 9). Evolution of the one-, two-, and three-pronged bacula are strangely analogous to the evolution of odd and even-toed feet in ungulates and they are no less adaptive.

Simple erection of the glans is requisite for intromission of the penis into the vagina. Secondary or second stage inflation of the glans simultaneous with pro-

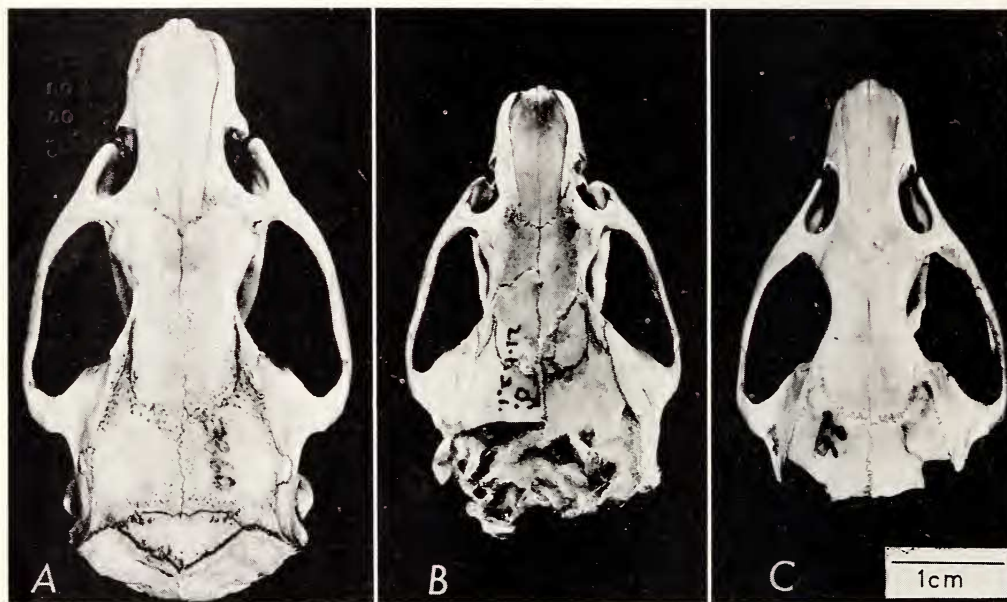


Plate 10. Skulls of *Kunsia*: A. *Kunsia tomentosus tomentosus*, adult; (San Joaquín, Bolivia); B. *Kunsia t. tomentosus*, juvenile cotype of *gnambiquarae* Miranda Ribeiro (Chapada, Brazil); C. *Kunsia fronto chacoensis*, type (Río de Oro, Argentina).

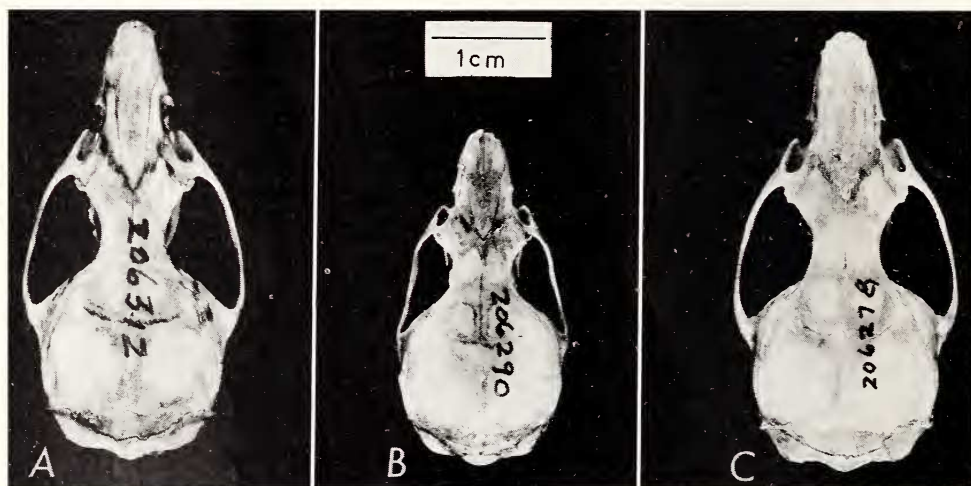


Plate 11. Skulls of *Scapteromys tumidus* from 3 km. east of Cardona, Uruguay; A. adult; B. juvenile; C. adult.

pulsion of the bacular complex and spreading of the bacular mounds (cf. BITTERA, 1918, pl. 3, fig. 12) facilitate passage of the glans through the cervix and ejaculation of sperm into the uterus. The complex glans penis is generally shorter than the simple glans and, presumably, is adapted to a short cervix. The longer glans of the simple penis presumably must negotiate a longer more elaborate cervix. Evolution of the simple penis from the complex may well be a response to selective pressures exerted by increasing elaboration of uterus and cervix. Hypothetically, at least, there exists a lock and key relationship between female and male genital tracts. The evolving uterus confers an advantage to the penis which unlocks the cervix and delivers the sperm.

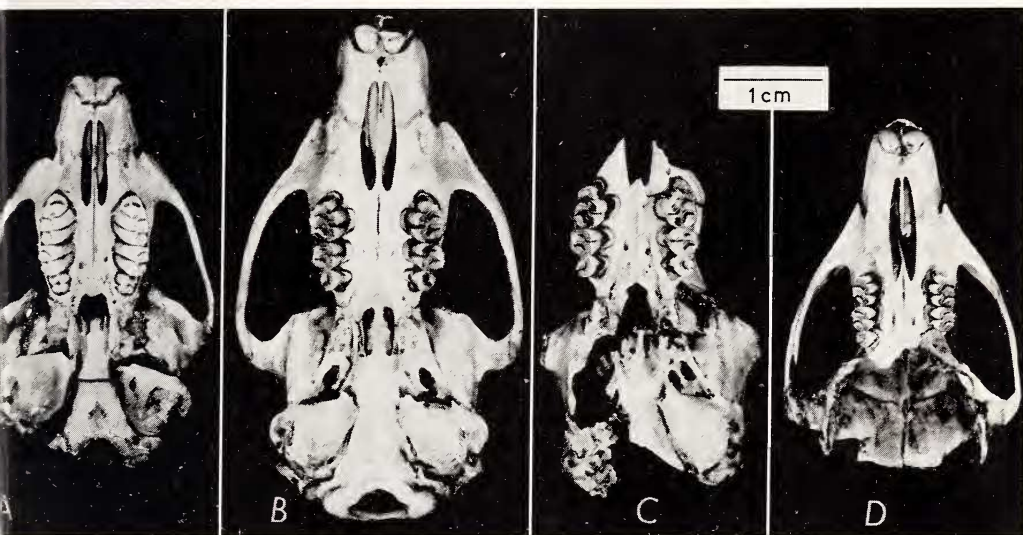


Plate 12. Skulls of *Kunsia*: A. *Kunsia tomentosus tomentosus*, juvenal cotype of *gnambiquarae*; B. adult (Bolivia); C. adult, type of *tomentosus* Lichtenstein; D. *fronto chacoensis*, type.

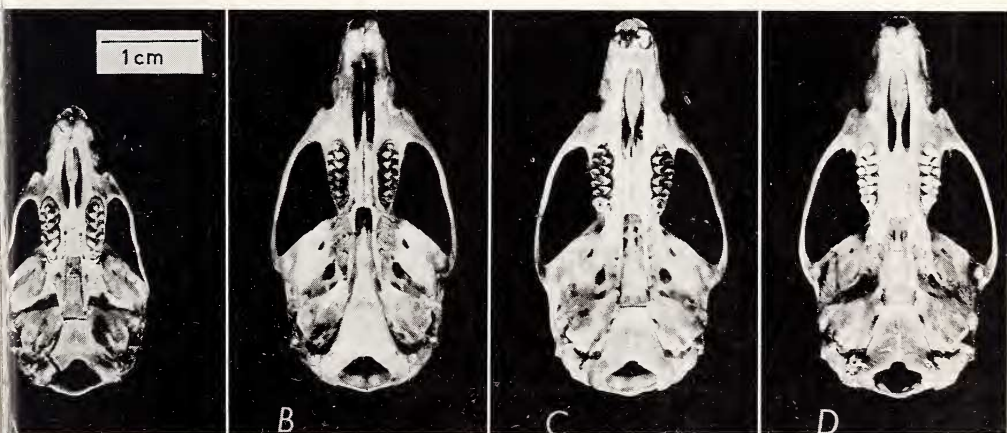


Plate 13. Skulls of *Scapteromys tumidus* from 3 km. east of Cardona, Uruguay: A. juvenal, B-D. adults.



## Summary

Scapteromyines are long-clawed palustrine, subaquatic and fossorial cricetine rodents confined to marshes, savannas and savanna-forest regions of southern Brazil, north-eastern Bolivia, most of Uruguay and the banks of the lower Ríos Paraná-Uruguay and Río de La Plata in Argentina. The genus *Scapteromys* comprises a single species, *S. tumidus*. The second scapteromyine genus, *Kunsia* (new), comprises *K. fronto* and *K. tomentosus*, which is the largest living cricetine. Modern scapteromyines are believed to have diverged from a moderately fossorial ancestor of akodont origin. *Scapteromys* invaded the bottomlands and became slightly shrew-like and adapted for subaquatic life. Its ancestral fossorial equipment has become attenuated or diverted to other uses. For example, the long claws, originally used for digging now serve primarily for seizing earthworm prey and for climbing into shrubs and trees during high floods. Parallel evolution between *Scapteromys* and similarly long-clawed oxymycterines is noted. *Kunsia*, on the other hand, has become frankly gopher-like with increasing specialization of the body, especially the head, teeth, feet and tail, for digging.

Part II discusses male phallic characters in murid, particularly cricetine, taxonomy. Some of the data is derived from the glans penises and bacula of *Scapteromys tumidus* and a few other South American cricetines. Most of the information used in the discussion, however, is contained in a series of papers on the glans penis by HOOPER and his collaborators, especially HOOPER and MUSSER (1964a). Two murid penis types are distinguished. The complex penis characterized by a three-pronged baculum is most primitive. It occurs in Old World and South American cricetines, gerbillines, microtines, murines and other murid groups not yet well studied. The simple penis, distinguished by a single-pronged baculum, is derived from the complex penis type. It characterizes twelve essentially Holarctic genera of cricetines known as the peromyscine group. Simplified or intermediate phalli also occur in one or more species of the otherwise complex penis groups of murids and a simple penis is common among non-murids. Evidently, the simple penis has arisen independently in all major assemblages of murids. The process of simplification is continuous, and irreversible. The result is a lock and key relationship produced by reciprocal selective pressures and responses between male and female genital tracts. Simplification of the penis may proceed

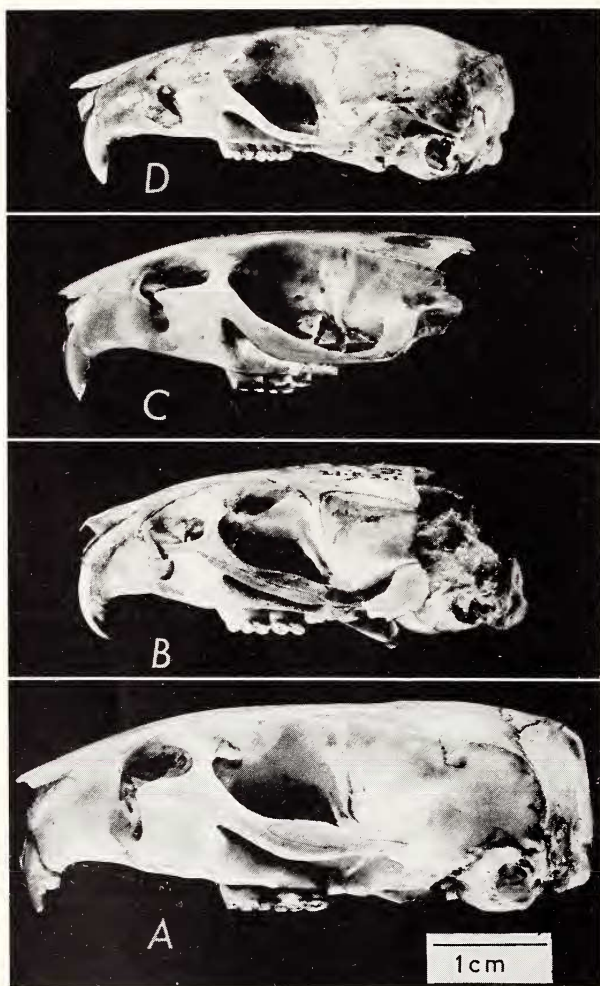


Plate 14. Skulls of scapteromyines: A. *Kunsia tomentosus tomentosus*, adult (Bolivia); B. juvenal, cotype of *gnambiquarae*; C. *Kunsia fronto chacoensis*, type; D. *Scapteromys tumidus* (3 km. east of Cardona, Uruguay).



by fusion of all bacular digits, by reduction and elimination of the lateral digits or by reduction and elimination of the middle digit only and fusion of the laterals. The several convergent paths leading to a simple penis suggest that the peromyscine group may be polyphyletic.

HOOPER and MUSSER (1964a) have assayed a classification of South American cricetines based on phallic characters only which makes a shambles of previous classifications founded on all the evidence. These authors' approach to systematics is strictly typological. They take no account of individual, local or geographic variations of the organ. Homology and homoplasy are not distinguished and they exclude from consideration the accumulated knowledge of the whole organism, its origin, evolution and dispersal.

A reexamination of current concepts of interrelationships between South American cricetines is made in the light of phallic characters defined by HOOPER and MUSSER. It is found that the glans penis is not the taxonomic touchstone these authorities believe it to be. Nevertheless, characters of the organ prove to be valuable adjuncts in the definition of many, perhaps most, species and genera of cricetines.

### Zusammenfassung

Scapteromyinae sind langkrallige, sumpfbewohnende, subaquatische und grabende cricetine Rodentier, die auf Sümpfe, Savannen und Savannenwald-Regionen von Süd-Brasilien, Nordost-Bolivien, den größten Teil von Uruguay und die Ufer des Rio Paraná in Uruguay und des Rio de la Plata in Argentinien beschränkt sind. Das Genus *Scapteromys* enthält nur eine einzige Species, *S. tumidus*. Das zweite scapteromyine Genus, *Kunsia* (gen. nov.) umfaßt *K. fronto* und *K. tomentosus*, den größten lebenden Cricetinen. Man nimmt an, daß die modernen Scapteromyinae sich abzweigten von in begrenztem Umfang grabenden Vorfahren akodonten Ursprungs. *Scapteromys* drang in die flachen Flußufer ein und wurde annähernd spitzmausartig und dem Wasserleben angepaßt. Die überkommene, dem Graben angepaßte

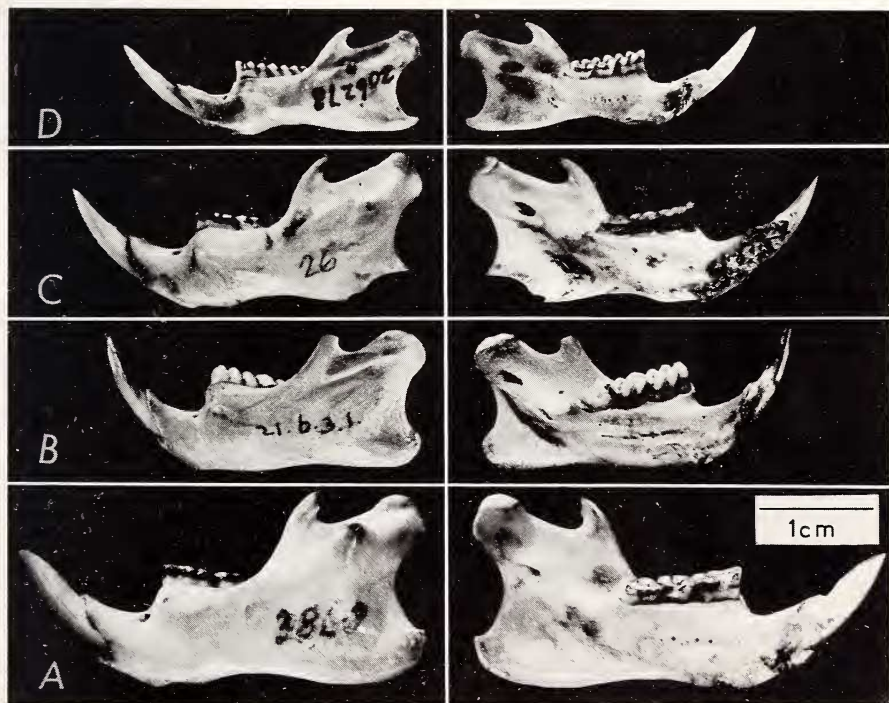


Plate 15. Mandibles of scapteromyines: A. *Kunsia tomentosus tomentosus* adult (Bolivia); B. juvenile, cotype of *gnambiquarae*; C. *Kunsia fronto chacoensis*, type; D. *Scapteromys tumidus* (3 km. east of Cardona, Uruguay).

Ausrüstung wurde weitgehend rückgebildet und anderen Zwecken dienstbar gemacht, so z. B. dienen die langen, ursprünglich zum Graben benutzten Krallen jetzt hauptsächlich dazu, Regenwürmer auszuwühlen und während des Hochwassers in Büsche und Bäume zu klettern. Parallelentwicklungen zwischen *Scapteromys* und ähnlich langkralligen Oxymycterinen werden angeführt. *Kunsia* andererseits wurde Gopher-ähnlich (Wühlratten-ähnlich) mit zunehmender Spezialisierung des Körpers, besonders des Kopfes, der Zähne und des Schwanzes zum Graben.

Im zweiten Teil der Arbeit wird der männliche Phallus-Character bei den Muriden, besonders den Cricetinen in bezug auf die Taxonomie diskutiert. Einige Daten wurden durch Glans und Baculum von *Scapteromys tumidus* gewonnen, desgleichen von einigen anderen südamerikanischen Cricetinen. Die meisten der in dieser Diskussion vorgebrachten Daten jedoch sind niedergelegt in einer Serie von Arbeiten über die Glans penis von HOOPER und seinen Mitarbeitern, besonders HOOPER and MUSSER (1964a). Es werden zwei muride Penis-

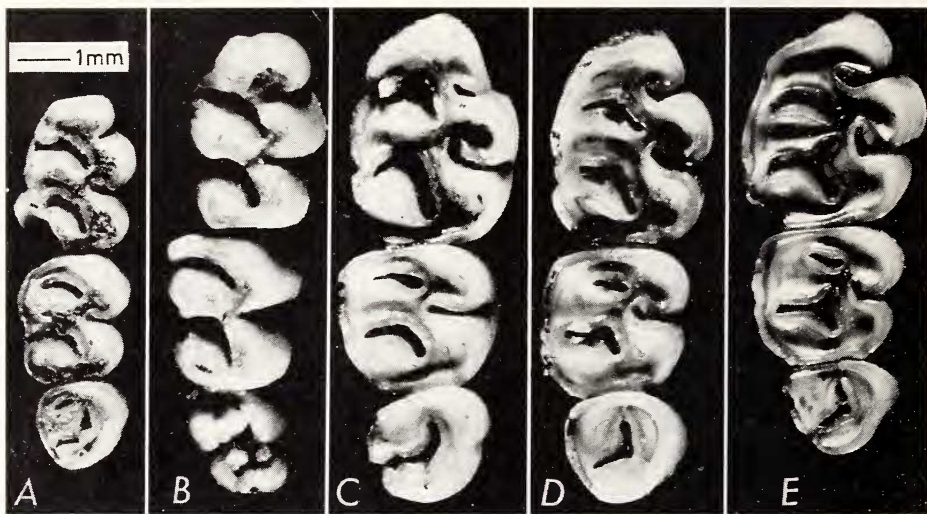


Plate 16. Right upper molars of scapteromyines: A. *Kunsia fronto chacoensis*, type; B. *Kunsia tomentosus tomentosus*, juvenile, cotype of *gnambiquarae*; C. *K. tomentosus*, type; D-E. adults (Bolivia).

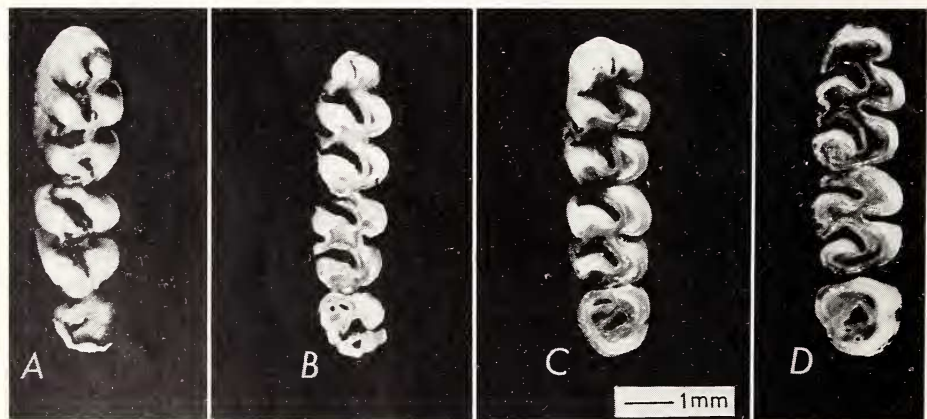


Plate 17. Right upper molars of *Scapteromys tumidus*; A. juvenile; B-D. adults (of same individuals shown in pl. 13).

Typen unterschieden. Der complexe Penis, charakterisiert durch ein dreifingriges Baculum, ist das primitivste. Es kommt vor in altweltlichen und in südamerikanischen Cricetinen, Gerbilliden, Microtinen, Murinen und anderen noch nicht gut untersuchten Murinen-Gruppen. Der einfache Penis, ausgezeichnet durch ein einspitziges Baculum, hat sich aus dem complexen Penistyp entwickelt. Es charakterisiert 12 im wesentlichen holarktische cricetine Genera, die als peromyscine Gruppe bekannt sind. Einfache oder intermediäre Phalli kommen ebenfalls vor bei einer oder mehreren Arten der sonst mit complexem Penis versehenen muriden Gruppen, auch ist ein einfacher Penis bei Nichtmuriden ganz allgemein. Offenbar hat sich der einfache Penis bei allen wichtigeren Muriden-Gruppen unabhängig entwickelt. Der Vereinfachungsprozeß hält an und ist irreversibel. Das Ergebnis ist eine Schloß-Schlüssel-Beziehung der männlichen und weiblichen Genitalien zueinander. Vereinfachung des Penis kann vor sich

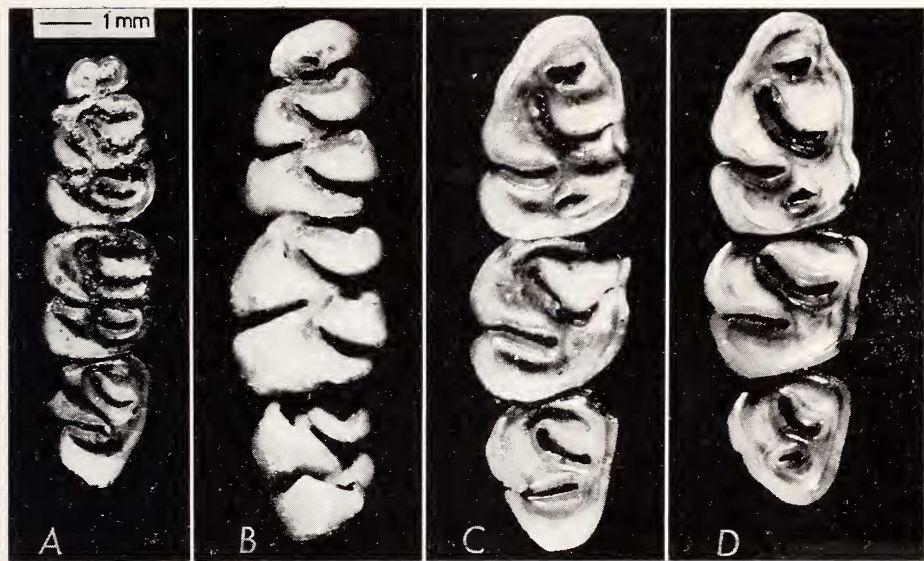


Plate 18. Left lower molars of *Kunsia*: A. *Kunsia fronto chacoensis*, type, B. *Kunsia tomentosus tomentosus*, juvenal cotype of *gnambiquarae*; C-D. adults (Bolivia).

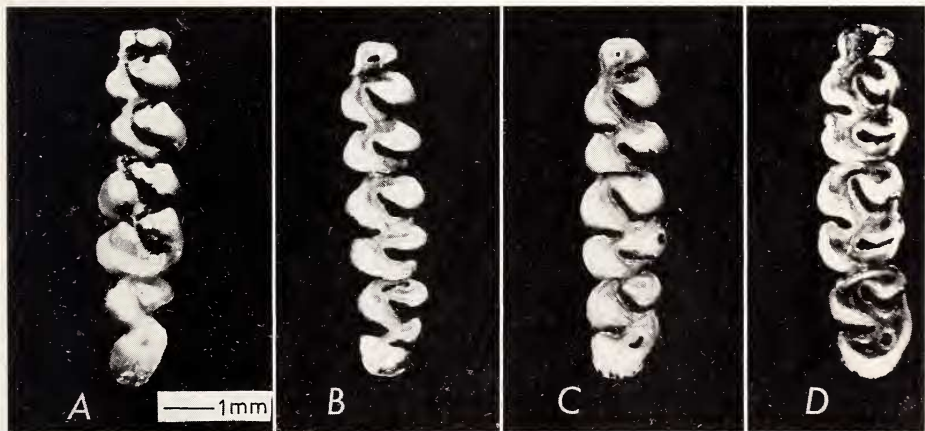


Plate 19. Left lower molars of *Scapteromys tumidus*; A. juvenal; B-D. adults (of same individual shown in pl. 17).



gehen durch Fusion aller 3 Finger des Baculums, durch Reduktion und Elimination der seitlichen Finger, oder durch Reduktion und Elimination nur des mittleren Fingers und Verschmelzen der beiden seitlichen. Die verschiedenen konvergenten Wege, die zu einem einfachen Penis führen, legen, die Vermutung nahe, daß die peromyscine Gruppe polyphyletischen Ursprungs sein dürfte.

HOOPER and MUSSER (1964a) haben versucht, eine Klassifikation der südamerikanischen Cricetinen nur nach den Verhältnissen der Phalli aufzustellen. Aber ihr Ergebnis widerspricht allen auf andere morphologische Tatsachen gestützten Klassifikationen. Die Autoren gehen die Systematik strikt typologisch an. Sie beachten keine individuellen, lokalen oder geographischen Variationen dieses Organs. Homologie und Homoplasie werden nicht unterschieden, und sie eliminieren aus ihren Betrachtungen die ganze bisherige Kenntnis vom ganzen Organismus, seinem Ursprung, seiner Entwicklung und Verbreitung.

Es wurde eine erneute Untersuchung der gängigen Auffassungen über Verwandtschaftsbeziehungen zwischen südamerikanischen Cricetinen unternommen und zwar unter Berücksichtigung der Phallus-Charaktere, wie sie von HOOPER and MUSSER definiert werden. Es erwies sich, daß die glans penis nicht der taxonomische Prüfstein ist, wie diese Autoren galuben. Nichtsdestoweniger erweisen sich die Charaktere dieses Organs als wertvolle Hilfe bei der Definition von vielen, vielleicht den meisten, Arten und Gattungen der Cricetinen.

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